ENTOMOLOGICA AMERICANA

VOLUME XXXIX

THE MORPHOLOGY, PHYLOGENY, AND HIGHER CLASSIFICATION OF THE FAMILY TINGIDAE, INCLUDING THE DESCRIPTION OF A NEW GENUS AND SPECIES OF THE SUBFAMILY VIANAIDINAE (HEMIPTERA: HETEROPTERA)[1]

By

CARL J. DRAKE
SMITHSONIAN INSTITUTION, WASHINGTON, D.C.

AND

NORMAN T. DAVIS
UNIVERSITY OF CONNECTICUT, STORRS, CONN.

TABLE OF CONTENTS

INTRODUCTION

Throughout the world the members of the Family Tingidae have generally been known by the common name of "lace-bug" ("Netz-wanzen," "masketaeger," "wantsje," *et cetera*) which character-izes them so well. Adults and nymphs are phytophagous and are generally rather host specific. Ordinarily they congregate on the under surfaces of leaves where their extraction of plant juices may cause a speckled discoloration and occasionally cause considerable damage to cultivated plants. They are widely distributed in the temperate and tropical regions of the world.

In the *Fauna Suecica*, Linnaeus (1746, pp. 207, 212) described the first two species of lace-bugs in his collective Genus *Cimex*. Twelve years later, both of these species were given trivial names and validated in *Systema Naturae* (Linnaeus, 1758, pp. 442, 443) under the technical names of *Cimex clavicornis* (fig. 2) and *Cimex Cardui* (fig. 1).

The Genus *Tingis* was created by Fabricius (1803, p. 124) to hold the Linnaean *Cimex clavicornis, Cimex Cardui,* and 9 other species. Of these 11 originally included species, only *Tingis cardui* (Linnaeus) at the present time remains in the Genus *Tingis. Cimex Cardui* Linnaeus was fixed as the type species of *Tingis* Fabricius by Latreille (1810, p. 433) and more than a century later substan-tiated by Direction 4 (1954, p. 53) of the International Commission of Zoological Nomenclature.

For more than a century, the proper orthographic spelling of the familial name of the lace-bugs was a subject of technical controversy among hemipterists. The contentions of the leading disputants finally were summarized and formally submitted to the Interna-
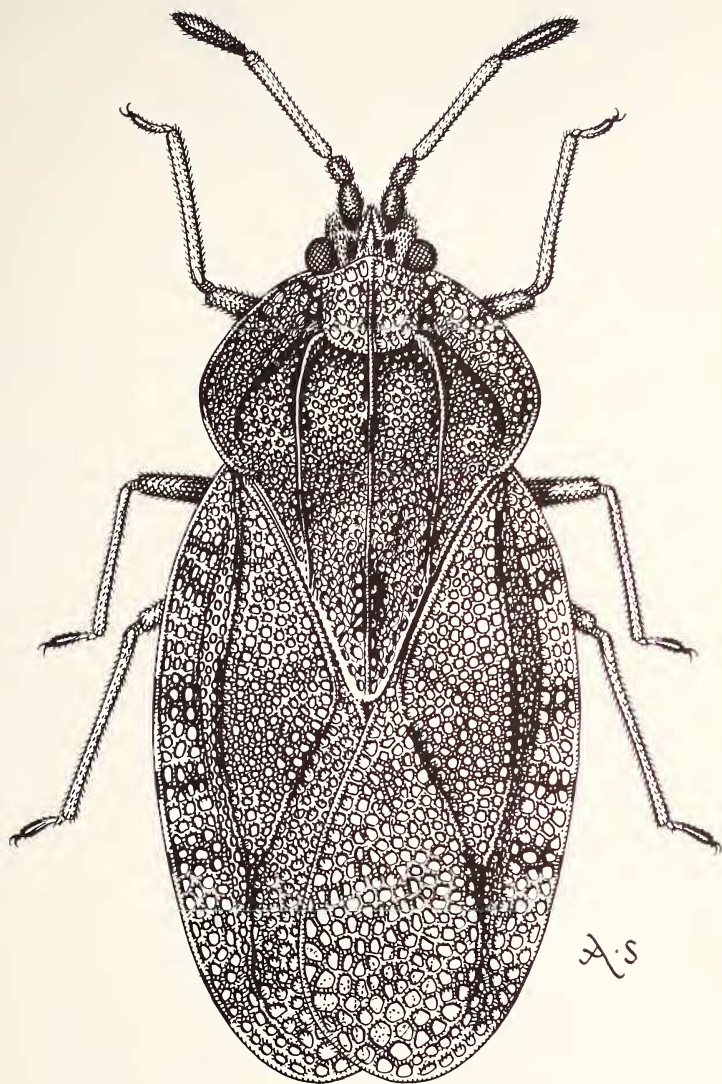
Fig. 1. *Tingis cardui* (Linnaeus).

tional Commission of Zoological Nomenclature with a request for a ruling on the origin, stem, and proper orthography of the family name of the lace-bugs based upon the Genus *Tingis* Fabricius (1803).

According to Opinion 143 (1943, pp. 83–85), quoted below:

"*Tingis* etant un nom latin dont le genitif est *Tingis* et l'accusatif Tingim. TINGIDAE est la forme correcte du nom de la famille."

And "the summary" (p. 84):

"The family name for Tingis Fabricius, 1803 (Syst. Rhyng.:124) in the Hemiptera is TINGIDAE."

Laporte (1833) created "Famille Tingidites" (French vernacular name) for the reception of the lace-bugs. In accordance with the provisions of the new Code of Zoological Nomenclature (15th International Congress of Zoology, London, 1958) we are accrediting the family "Tingidae" to Laporte.

The formation of the familial group (superfamily, family, and subfamily) for the lace-bugs embodies anatomical and physiological problems not unlike those encountered in the setting up of other families in the Order Hemiptera. To bring out clearly the historic creation and evolutionary development of the family concept in tingids, we have prepared the bibliography that follows:

Concepts of the Family Tingidae Laporte, 1833

Famille Zoathelga Dumeril, 1806, p. 264.

Familia Cimicides Latreille, 1807, p. 126 (*Tingis,* p. 139).

Divisio Frontirostres, Familia Cimicides Fallén, 1814, pp. 3, 4.

Tribus Heterata, Legio Terrestria, Natio Cimicides Billberg, 1820, pp. 66, 67.

Familie Geocorisae, Zunst Membranaceae Latreille, 1825, pp. 419, 422.

Familie Geocorisae, Zunst Membranaceae Berthold, 1827, pp. 415, 420.

Sectio Hemelytrata, Divisio Frontirostres, Familia Cimicides Fallén, 1829, pp. 7, 142.

Famille Geocorises Latreille, 1829, p. 201.

Famille Tingidites Laporte, 1833, p. 47.

Zunst Geocores, Familie Membranacei Burmeister, 1835, pp. 203, 249.

Tribu Géocorizes, Famille Tingidites Spinola, 1837, pp. 67, 68, 161.

Fig. 2. *Copium clavicornis* (Linnaeus).

Familia Tingini Costa, 1838, p. 20.

Tribu Géocorizes, Famille Tingidites Spinola, 1840, pp. 67, 161.

Family Tingidae Westwood, 1840, p. 447, p. 120 (Synopsis); Hurd, 1946, p. 437; Monte, 1947, p. 2; China and Miller, 1959, p. 261; Takeya, 1951, p. 5; Drake and Ruhoff, 1960 (in press).

Section Géocorises, Famille Ductirostri, Groupe Tingides Amyot and Serville, 1843, pp. xv, xl, 285, 295.

Zunst Geocores, Familie Tingideae Fieber, 1844, pp. 20, 27.

Sectio Geocorisae, Familia Ductirostri, Tribus Membranacei Sahlberg, 1848, pp. 1, 9, 14, 125, 127.

Familia Tingiditae Spinola, 1850, p. 27.

Sectio Gymnocerata, Subsectio Geodromica, Familie Tingididea Fieber, 1851, p. 9.

Familie Harpagocorisiae, Tribus Geocorisiae, Scolymophilae Kolenati, 1856, pp. 419, 420.

Familia Tingidae Costa, 1855, p. 293.

Familia Membranacei Stål, 1859, p. 259.

Sectio Geodromica, Zunst Gymnocerata, Familie Tingididea Flor, 1860, pp. 61, 63, 65, 317.

Familia Tingitidea Costa, 1860, p. 6.

Sectio Gymnocerata, Subsectio Geodromica, Familia Tingididae Fieber, 1861, pp. 22, 35, 116, 400.

Section Tingidina, Family Agrammidae and Family Tingididae Douglas and Scott, 1865, pp. 23, 24, 242, 243.

Familia Tingidida Stål, 1865, p. 25.

Familia Tingini Stål, 1871, p. 671.

Familia Tingitidae, subfamilia Tingitina Stål, 1873, pp. 115, 116; 1874, pp. 43, 45.

Sectio Geodromica, Tribus Tesseratomida, Familia Tingidida Ferrari, 1874, pp. 118, 133, 168.

Sectio Gymnocerata, Familia Tingidae Siebke, 1874, pp. 1, 22.

Familia Tingididea Vollenhoven, 1878, p. 265.

Section Geocores ou Gymnocerata, Famille Tingidides, tribu Tingini Puton, 1879, pp. 83, 87.

Family Tingitidae Uhler, 1886, p. 21; Champion, 1897, pp. 1, 2; Horváth, 1906, p. 1; 1911, p. 14; Drake and Poor, 1936, p. 382; China, 1943, p. 245.

Famille Tingidae Lethierry et Severin, 1896, pp. 1, 4.

Section Geocorisae, Famille Tingidides Puton, 1899, pp. 5, 38.

Division Trochalopoda, Superfamily Cimicoideae, Family Tingidae Kirkaldy, 1908, pp. 359, 360.

Familie Tingididae Oshanin, 1908, p. 395.

Series Onychiophora, Superfamilie Neidodeae, Phalanx Neidiformes,

Familie Tingididae Reuter, 1910, pp. 75, 76, 77.

Series Onychiophora, Phalanx Lygaeiformes, Superfamilie Tingitoideae, Familie Tingitidae Oshanin, 1912, pp. 26, 27, 41, 42.

Series Anonychia, Phalanx Henicocephaliformis, Superfamilie Tingitoidea, Familie Tingidae Reuter, 1912, pp. 27, 49.

Series Anonychia, Family Tingididae Van Duzee, 1916, p. 25; 1917, p. 209.

Phalanx Pyrrhocoriformes, Series Anonychia, Superfamily Tingitoideae, Family Tingitidae Singh-Pruthi, 1925, pp. 161, 163.

überfamilie Geocorisae (Gymnocerata), Familienreihe Pentomoidea, Unterreihe Tingini, Familie Tingidae Börner, 1934, p. 144.

Sous-order Geocorises, Superfamille Tingitoidea, Famille Tingitidae Poisson, 1951, p. 1798.

Serie Onychiophora, Superfamilia Tingitoidea, Familia Tingidae Gomez-Menor, 1956, p. 139.

Geocorisa, Family Tingidae and Family Vianaididae China and Miller, 1959, pp. 18, 20, 34.

The foundation of tingid hierarchy was laid down by the eminent hemipterist Stål (1873, pp. 115; 1874, p. 45) nearly a century ago. Among other foremost specialists after Stål, Reuter (1912) and Horvath (1906) have contributed vastly to our knowledge of the classification of the lace-bugs. The taxonomic paper by Fieber (1844) entitled *"Monographie der Tingideae"* is international in scope and contains fine figures of a large number of rare and little-known species of Tingidae.

Laporte (1833, pp. 47, 48) included the Genus *Piesma* in the Family Tingidides. Stål (1873) separated the Family Tingitidae, as it was then constituted, into the Subfamilies Tingitina and Piesmina, and divided the Subfamily Tingitina into the divisions Cantacaderaria, Serenthiaria, and Tingitaria. Distant (1909, pp. 121, 122) added the divisions Axiokersosaria and Aidoneusaria for new genera and species from India. Reuter (1912, pp. 27, 49) formed the Superfamily Tingidoideae to hold the Families Piesmidae and Tingididae.

Up to now, following Stål's classification, lace-bugs have been known as the Family Tingidae, and separated into the Subfamilies Tinginae, Cantacaderinae, and Agrammatinae (*olim* Serenthiinae). Distant's divisions of Axiokersosaria and Aidoneusaria recently have been suppressed as synonyms of the Subfamily Tinginae (Drake and Ruhoff, in press). Tullgren (1908), Leston, Pendergrast, and Southwood (1954), Pendergrast (1957), and others have

7

presented anatomical evidences to show that the Superfamily Tingoidea is not a natural group and that the Tingidae belong to the Cimicomorpha and the Piesmatidae to the Pentatomomorpha. The piesmatines are most closely related to the Family Lygaeidae and appear to have affinities with the Cyminae of that family (Drake and Davis, 1958).

HIERARCHAL CHANGES

Based on detailed studies of their morphology and systematics, several changes in the major classification of the tingids appear in the pages to come. The following is a brief prospectus of these changes: 1) the suppression of the Subfamily Agramminae Westwood as synonymous with the Subfamily Tinginae Laporte; 2) the lowering of the Family Vianaididae Kormilev to that of Subfamily Vianaidinae Kormilev and the transferring the latter and its components to the Family Tingidae; and 3) the proposing of the Superfamily Miroidea Hahn (*sensu novem*) to hold the Families Miridae Hahn (1831) and Tingidae Laporte (1833). Under this new systematic arrangement, the Family Tingidae comprises the Subfamilies Tinginae Laporte, Cantacaderinae Stål, and Vianaidinae Kormilev. In addition two tribes, Cantacaderini Stål and the Phatnomini, new tribe, are designated in the Subfamily Cantacaderinae.

At the generic and specific level several other taxonomic changes are consummated. The Genus *Vianaida* Kormilev is treated as a junior synonym of the Genus *Anommatocoris* China and this genus now comprises *A. minutissimus* China and *A. coleoptratus* (Kormilev). A new genus and species, *Thaumamannia manni*, from Bolivia is described.

GENERAL MORPHOLOGY

Head. The shape of the tingid head is usually short and declivent (figs. 3, 5, 33, 34) although in the Cantacaderinae (figs. 28, 29, 30, 31) and in several genera of Tinginae (*Biskira* Puton; *Dictyonota* Curtis, fig. 35; *Ypsotingis* Drake, fig. 36; and *Dictyotingis* Drake, fig. 37 for examples), it is quite long and moderately porrect. However, the head at times may appear to be less declivent than it actually is because of the forward extension of the bucculae (fig. 6, Buc).

The head is inserted into the prothorax up to the compound eyes (figs. 3, 6, 31) and often bears a series of processes on its dorsal surface. These processes vary in form from short, blunt tubercles (figs. 36, 38) to very long, sharp spines (fig. 42), and extend anteriorly in a porrect, decumbent, or almost upright position. Up to nine processes may occur and may be designated as the occipital, frontal, and genal pairs and three median processes. The paired and median processes occur independently of each other.

The dorsal cephalic processes range from 0 to 9 in the Cantacaderinae (figs. 28, 30, 31). The number in the Tinginae generally varies from 0 to 5 and consist of the frontal and occipital pairs and a single median process (figs. 38, 39, 42)[1]. The median process is very often situated just behind the frontal pair, thus forming a compact group of three (fig. 55), although not infrequently it is placed more posteriorly near the center of the vertex (fig. 41). In the Genus *Belenus* Distant, the cephalic processes are sometimes branched or forked.

The juga are never strongly produced; the ocelli are always absent; and the compound eyes (fig. 45) are characteristically strongly convex and widely separated from each other. The bucculae are almost always well developed, areolate and long; their anterior ends may or may not converge and meet in front of the labium so as to close the buccal sulcus. However, in some Tinginae (e.g., in the Genera *Aconchus* Horvath and *Dulinius* Distant) the bucculae terminate anteriorly along the lateral sides of the beak. In many genera of Cantacaderinae (figs. 6, 28) the bucculae surpass the apex of the tylus. Posteriorly, the bucculae extend backwards to or slightly on to the prosternum (figs. 41*b*, 45*b*).

Labium. The labium is four-segmented and none of the segments shows marked reduction (figs. 4, 5, 6). It varies in length in different species, its apex terminating on the thoracic sterna or any one of the pregenital abdominal segments and in a few instances (e.g., species of *Ypsotingis* Drake of the Tinginae and *Teratocater* Drake and *Allocader* Drake of the Cantacaderinae) the labium extends as far back as the first genital segment. The "beaks" of the cantacaderines average longer than those of the Tinginae. In the vianaidines the "beaks" of all species so far described extend beyond the metasternum to the third or fourth abdominal sternum (fig. 5).

---

[1] However, in the tingine Genus *Ogygotingis* Drake (Fig. 41) there are 7 processes including a genal pair.
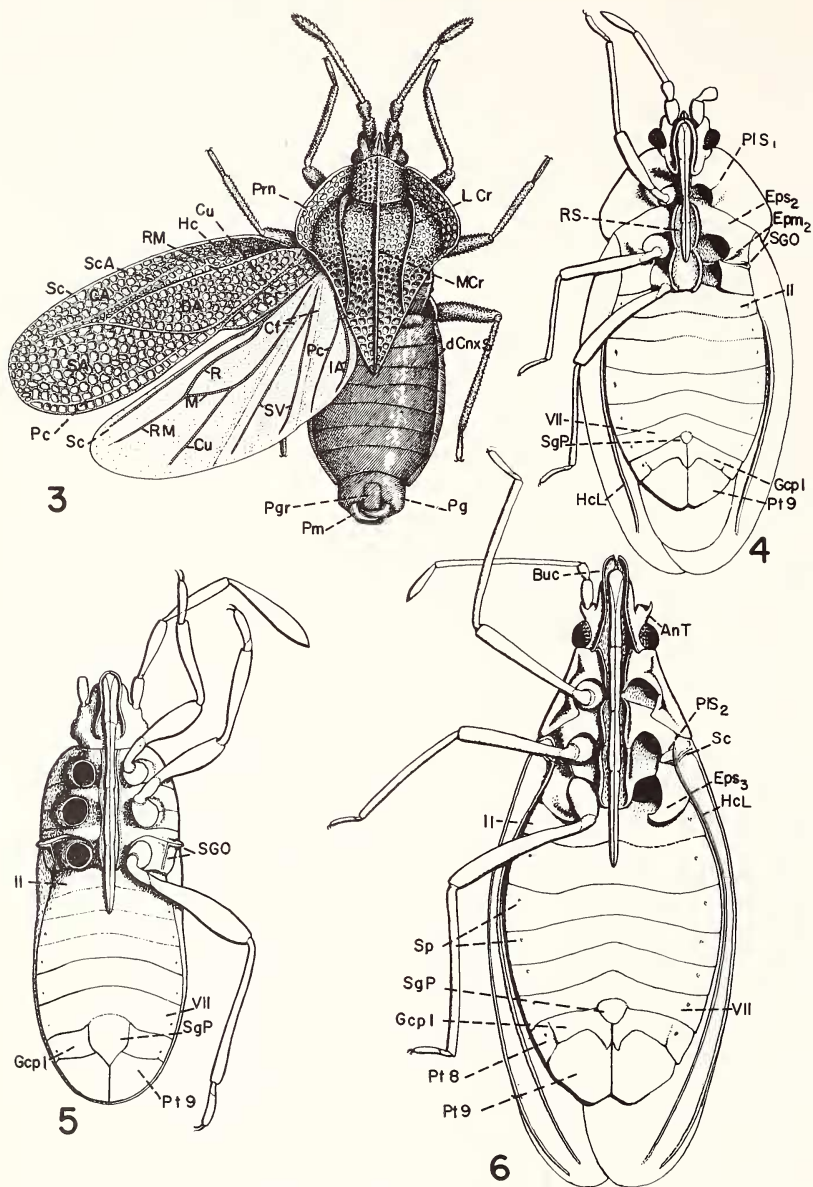
Fig. 3. *Tingis cardui* (Linnaeus), male with left wings extended and right wings removed to expose abdomen. **CA,** costal area; **Cf.** cubital furrow; **CL,** clavus; **Cu,** cubitus; **DA,** discoidal

Antennae. The antennae are four-segmented and range from slender (fig. 49) to stout (fig. 67), from short (fig. 47) to long (fig. 46), and from smooth (fig. 66) to hairy (fig. 63).

In the gall-making Genus *Onymochila* Drake (fig. 50), the antennae are moderately slender. Conversely, the only other genera of gall-forming tingids, *Copium* Thunberg (fig. 2) and *Paracopium* Distant (fig. 52), have very thick and heavy antennae. Since the members of these three genera are the only true gall-making species in the Family Tingidae, or even in the order Hemiptera-Heteroptera, we are including illustrations to show the two types of galls formed by the species of the Genera *Paracopium* (fig. 52) and *Onymochila* (fig. 50), respectively. According to the literature, the galls formed by *Copium* and *Paracopium* result in the castration of the floral generative organs.

The first segment varies from short (fig. 47) to long (figs. 41, 46); the second is almost invariably the shortest, although at times both segments are short and subequal in length and moniliform or subglobose in shape (figs. 65, 68). The third segment is almost always the longest. (In a few genera such as *Mecopharsa* Drake the third and fourth segments are subequal in length. See figs. 48,

---

area; **dCnxS**, dorsal connexival suture; **Hc**, hypocosta; **LCr**, lateral carina; **M**, media; **MCr**, median carina; **Pc**, postcubitus; **Pg**, pygophore; **Pgr**, proctager; **Pm**, paramere; **Prn**, paranotum; **R**, radius; **RM**, fused radius and media; **SA**, sutural area; **Sc**, subcosta; **ScA**, subcostal area; **SV**, secondary veins; **1A**, first anal vein.

Fig. 4. *Tingis cardui* (Linnaeus), ventral aspect of female with left legs removed to expose coxal cavities. **Epm$_2$**, mesoepimeron; **Eps$_2$**, mesoepisternum; **Gcp 1**, first conocoxopodite; **HcL**, hypocostal lamina; **PlS$_1$**, propleural suture, **Pt 9**, ninth paratergite; **RS**, rostral sulcus; **SGO**, scent gland ostiole; **SgP**, subgenital plate, **II–VII**, abdominal segments.

Fig. 5. *Anommatocoris coleoptratus* (Kormilev), ventral aspect of female with right legs removed to expose coxal cavities. **Gcp 1**, first gonocoxopodite; **Pt 9**, ninth paratergite; **SGO**, scent gland opening; **SgP**, subgenital plate; **II–VII**, abdominal segments.

Fig. 6. *Cantacader quadricornis* (LePeletier and Serville), ventral aspect of female with left legs removed to expose coxal cavities. **AnT**, antennal tubercles; **Buc**, buccula; **Eps$_3$**, metepisternum; **Gcp 1**, first gonocoxopodite; **HcL**, hypocostal lamina; **PlS$_2$**, mesopleural suture; **Pt 8**, eighth paratergite; **Pt 9**, ninth paratergite; **SgP**, subgenital plate; **Sp**, spiracles, **II–VII**, abdominal segments.

49). The fourth segment also varies in length and thickness from moderately short and fusiform or clavate to very long and slender (figs. 4, 48).

Thorax. No other hemipteran family exhibits such a vast series of spectacular pronotal structures, augmented by tumid elevations of the elytra, as do the Tingidae (figs. 44, 54–59, 71, e.g.) whose remarkable diversities are hardly surpassed even by the homopteran Family Membracidae. The pronotum may be flat (fig. 38) or convex (figs. 64, 65), finely or coarsely punctate (figs. 36, 61, 71), with or without lateral expansions, or paranota (figs. 39, 64, 65, 66), with the collum simple (figs. 38, 70), or inflated (figs. 53, 54, 58, 68, 71), with longitudinal carinae present, in combinations of one, three, or five, and with the hind margin usually triangularly extended backwards (figs. 67, 71), but at times abbreviated and truncated posteriorly (fig. 63).

Of the subfamilies, the Tinginae possess the more varied, the most enormously developed and the most curiously modified pronotal structures. Either one or three pronotal carinae are present, and these may be simple ridges (figs. 38, 49) or elevated and variously modified (figs. 57, 62 for examples). In several genera, such as *Aepycysta* Drake and Bruner (fig. 59), *Habrochila* Horvath, and *Dulinius* Distant the posterior projection of the pronotum is strongly inflated; the lateral carinae may be low and ridgelike, foliaceously elevated and laminiform, auriculate, conchate, subglobose, and various other shapes. Moreover, the paranota may be absent (figs. 39, 65), narrow, wide, reflexed, or may be variously modified as depicted in the illustrations (figs. 54, 55, 61, 69, 75 for a few examples).

In the Cantacaderinae, the pronotum may be uni- (fig. 29), tri- (fig. 30), or quinquecarinate (fig. 28); the paranota are narrow (fig. 31) or widely expanded (fig. 30); the collum is plain (fig. 29) or provided with an inflated hood (fig. 30); and the posterior margin of the pronotum is subtruncate and often slightly sinuate. The scutellum may be either visible (fig. 31) or concealed (fig. 28) by the pronotum.

The procoxal cavities are almost always open behind and on their lateral margin a small indentation and groove mark the position of the obsolete pleural suture (fig. 4, PlS_1). The labial sulcus extends over the thoracic sterna and is bordered by areolated laminae on each side similar to the bucculae. The meso- and metathorax are firmly united ventrally and the intersegmental boundary is indicated internally by a ridge between the mesocoxal cavities (fig. 7). Laterally, this ridge becomes a suture passing just behind the

mesocoxal cavities and then dorsally along the scent gland ostioles to the tergum. As in the prothorax, the mesopleural suture is indicated by a short groove extending dorsally from the edge of the coxal cavity (fig. 6, PlS_2). However, it does not extend to the pleural wing process and so the mesepisternum and mesepimeron are incompletely differentiated.

The metapleural suture is concealed since the metepisternum has enlarged, displacing and overlapping the small metepimeron (fig. 6, Eps_3). In fact the posterior edge of the metepisternum forms a flange extending over the base of the abdomen and hind coxa.

Legs. The legs are in general isomorphous and lack distinctive spines; the femora are never strongly swollen (figs. 4, 5, 6). The coxae are more or less globose, or conical and convergent. The hind coxae may be classed as the rotary type (*in sensu* Schiödte, 1870). The tarsi are two-segmented, and the basal segment is small and may be partly fused to the distal segment. The claws lack arolia and pseudoarolia, but usually have a small cusp on their inner basal edge.

Thoracic Scent Glands. These glands consist of two elongate diverticula (fig. 7, **SGD**) which open on each side near the margin of the metacoxal cavities. The orifice of each is at the base of a groove that passes upwards on to the metapleuron and there expands to form the scent gland ostiole (fig. 4, **SGO**). In the Cantacaderinae the orifice is at the base of the metasternal apophysis as it is in most Heteroptera (Brindley, 1930), but in the Tinginae the orifice has moved posterior to the apophysis and in some genera (*Tingis*) lies on the dorsal posterior margin of the coxal cavity, (fig. 7). In these forms the external groove of the scent gland apparatus passes from the orifice ventrally along the margin of the coxal cavity and thence dorsally into the ostiole.

The metathoracic glands appear to be very specialized and somewhat unique. In the more generalized Heteroptera the scent gland apparatus consists of a median invagination which forms a broad pouch-like reservoir. Arising from this reservoir is a pair of tubular glands. In the tingids it appears that the median portion of the invagination has been obliterated leaving only lateral sacs.

Mesothoracic Wing. Pterygopolymorphism is by no means uncommon in the Tingidae. Brachyptery is expressed by the shortening of the forewings, the reduction or absence of the hind wings, and the less convex thorax.

That part of the mesothoracic wing which is ordinarily membraneous in the Heteroptera is, in tingids, of the same lace-like, reticulate texture as in the corium. Like the pronotal structures,

13

Fig. 7. Pterothoracic sternum and scent glands of *T. cardui* from above. **CxC**$_{2-3}$, coxal cavities; **EpS**$_3$, metepisternum; **SAp**, sternal apophysis; **SGD**, scent gland diverticulum.

Fig. 8. Dorsal aspect of *T. cardui* pygophore with dorsal wall removed to expose phallus. **Pg**, pygophore; **Phl**, phallus; **SAr**, suspensory arms.

Fig. 9. Lateral aspect of *T. cardui* abdomen with ovipositor extended. **Gap 3**, third gonapophysis; **Gcp 1**, first gonocoxopodite; **Gcp 2**, second gonocoxopodite; **Ovp**, ovipositor; **Pt 9**, ninth paratergite; **SgP** subgenital plate; **VII**, seventh abdominal segment.

Fig. 10. Inner aspect of the female genitalia of *T. cardui*. **Gap 1**, first gonapophysis; **Gap 2**, second gonapophysis; **Gap 3**, third gonapophysis; **Gcp 2**, second gonocoxopodite; **Ra 1**, first ramus; **Ra 2**, second ramus; **RaP**, ramal plate.

Fig. 11. Dorsal aspect of terminal abdominal segments of male *C. quadricornis*. **Pgr**, proctiger; **Pg**, pygophore; **Pm**, paramere.

Fig. 12. Dorsal aspect of the female genital apparatus of *T. cardui*. **GCh**, genital chamber; **OdC**, common oviduct; **OdL**, lateral oviduct; **Ra 1**, first ramus; **RaP**, ramal plate; **SS**, seminal sac.

Fig. 13. Forewing of *C. quadricornis*. **CA**, costal area; **Cl**, clavus; **Cu**, cubitus; **DA**, discoidal area; **Hc**, hypocosta; **RM**, radius-media; **SA**, sutural area; **Sc**, subcosta; **ScA**, subcostal area; **STA**, stenocostal area.

Fig. 14. Metathoracic wing of *C. quadricornis*. **CF**, cubital furrow; **Cu**, cubitus; **M**, media; **Pc**, postcubitus; **R**, radius; **RM**, radius media; **RSc**, radius-subcosta; **Sc**, subcosta; **SV**, secondary veins; **1A**, 1st anal vein.

Fig. 15. Dorsal aspect of the genital apparatus of *C. quadricornis*. **a**, sclerotized ring; **GCh**, genital chamber; **OdL**, lateral oviduct; **Ra 1**, first ramus; **Spt**, spermathecal gland.
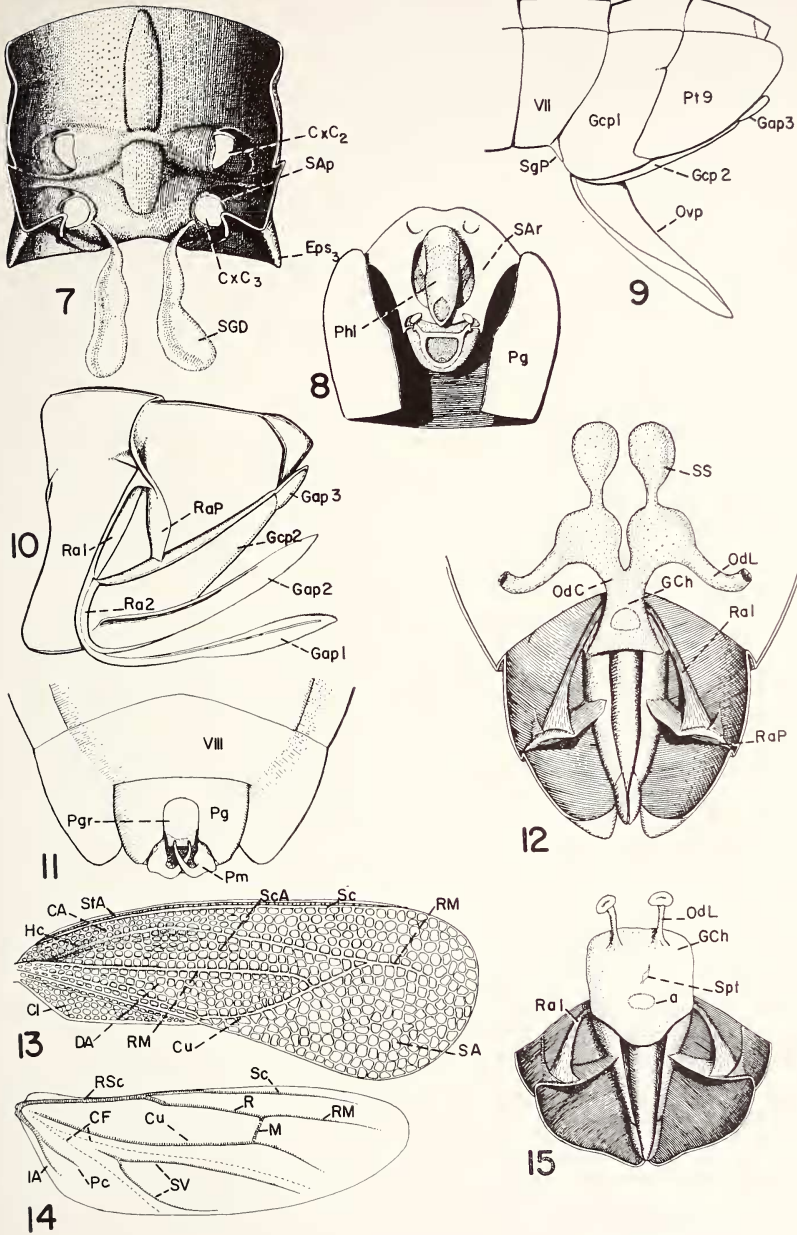
there is variety in the form and texture of the forewing; some genera have forewings that are coarsely and closely reticulated and thus appear almost coriaceous, whereas those of many other genera have fine reticulation and larger areolae, which makes them appear much more membraneous and delicately lacy. Differences in the thickness of veinlets and the size of areolae are characters that grade with one another on the generic level.

In the macropterous forms of the Tinginae, the clavus is present but much reduced in size and concealed beneath the posterior process of the pronotum. In contrast, the clavus is always visible in all pterygopolymorphic forms in the Cantacaderinae, although at times it is fused with and then not always sharply delimited from the discoidal area (figs. 29, 30).

Generally, three longitudinal veins extend through the corium (fig. 3), dividing it into what are customarily known as the costal (**CA**), subcostal (**ScA**), discoidal (**DA**), and sutural (**SA**) areas. The median vein (**RM**) is the most distinct and a comparison of tingids with other Heteroptera indicates that it is the fused radius and media. It is followed by the cubitus (**Cu**) which lies very close to the claval furrow. The identity of the veins anterior to **RM** is less certain and needs further consideration.

Handlirsh (1908) and Tanaka (1926) interpret the heteropteran wing as lacking a costal vein since the costal trachea is vestigal or absent. Thus the vein on or near the costal margin is generally considered to be the subcosta; this position is shown in several cimicoids by China and Myers (1929, p. 111). If the vein lying along the anterior margin of the subcostal area of tingids is **Sc** then its position is unusual since it is well removed from the costal margin. Evidence contrary to this interpretation is found in some Cantacaderinae (Genera *Cantacader* Amyot and Serville, *Ceratocader* Drake, *Teratocader* Drake, and *Allocader* Drake to exemplify), where an additional vein lies just behind the costal margin (fig. 13, **Sc**). It seems most likely that this vein is the subcosta, and that in the Tinginae the subcosta probably lies on the costal margin.

If our interpretation of **Sc** and **RM** is correct, then there appears to be an extra vein between **Sc** and **RM**. On the dorsal surface this vein is strongly depressed forming a channel between the so-called costal and subcostal areas. Ventrally, it is elevated as a distinct ridge which overlaps the connexivum and thus encloses the edge of the abdomen. An indication of the possible origin of this structure may be found by studying the costal margin of various other cimicomorphs. In such groups as nabids, reduviids, and thaumastocorids, the proximal costal margin is generally deflected

16

downward over the thorax and, at most, over the anterior lateral edge of the abdomen. The shoulder on the hemelytron thusly formed is evenly rounded; the subcosta apparently follows the reflected margin and passes laterally with it.

In anthocorids, microphysids, isometopines, and most mirids the proximal costal margin generally is sharply reflected ventrad and the shoulder of the hemelytron has an acute rather than a rounded edge. In these groups, the costal margin is often reflected as far posteriorly as the node, although it gradually diminishes posteriorly. In *Anthocoris*, China and Myers (1929, p. 112) have indicated that "Basally **Sc** is practically coincident with the turned-over costal margin, but before the node is reached this vein passes inwards (*i.e.*, to the new edge of the wing, with which it is coincident to the node)." Thus we see an indication of a separation of the subcosta and the original costal margin and of the latter's remaining on the ventral surface of the wing. The structure formed by the apparent shift in the position of the costal margin is termed here the hypocostal lamina.

Dorsally, at the base of the hemelytron of the cimicomorpha having a hypocostal lamina, there is usually a distinct sulcus coincident with this lamina. China and Myers (1929, p. 113) have pointed out that this groove is especially prominent in the mirid Genera *Pycnoderes, Eurychilopterella, Hyaloides,* and *Stethoconus* in which it appears to be a vein between **Sc** and **RM**. These authors do not consider it to be a true vein. The vein-like appearance of the hypocosta is most pronounced in *Hyaloides* with its semitransparent hemelytra. In these mirids the hypocosta remains ventral and terminates abruptly at the cuneus, and there is an expanded dorsally reflected cell-like area between the hypocostal lamina and the leading edge of the wing. A similar condition is found in the velocipedid, *Scotomedes,* in which the hypocosta is also vein-like and the edge of the hemelytron is expanded, forming a broad flange.

Returning again to the cantacaderine forewing, we can see that at the wing base the costal margin is acutely reflected ventrad (fig. 6, **HcL**). The vein which we have designated as the subcosta, originates on this costal margin but abruptly turns upward to run near the acute leading edge of the wing (**Sc**). The costal margin, however, remains ventral and extends to near the apex of the wing. The leading edge of the wing is expanded and there is a dorsally reflected area, the so-called costal area, which is equivalent to the expanded costal margin of the wing of *Hyaloides* and *Scotomedes*. In many of the Tinginae the expansion of the costal area is even more pronounced (figs. 38, 49, 60, 61).

This apparent reversal in position of the **Sc** and costal margin creates obvious problems in nomenclature which seem best resolved by naming the ventrally shifted costal margin the hypocostal lamina, and the coincident vein-like structure on the dorsal surface, the hypocosta. Since the names of the areas of the wing are well established in the literature and somewhat arbitrary, there is no need to change them to conform with the venation terminology. The narrow area set off by the subcosta of some Cantacaderinae is useful taxonomically and will be designated here the stenocostal area.

The foregoing interpretation of the venation of the hemelytron of tingids seems to best fit the facts at hand but should not be considered conclusive since further comparative and developmental studies of the venation are needed.

Metathoracic Wings. Along the proximal costal margin of the tingid hind wing there is a strong vein which, in Heteroptera generally, is interpreted as being the fused subcosta and radius (fig. 14, **RSc**). After running about a third of the length of the wing, these veins separate; the **Sc** remains close to the costal margin, while **R** passes inward. **Sc** just beyond its separation from **R** is very concave and this concavity is a part of the apparatus by which the fore and hind wing are coupled. The radius, just beyond its separation from **Sc**, abruptly changes from a biconvex vein into a thin, much weaker vein; this point of change is termed the *caesura*.

Following **R** there is another longitudinal vein generally interpreted as the cubitus (**Cu**). This vein is weak proximally but becomes more distinct distally. It is joined to **R** by a diagonal vein which probably is the media. After **M** has joined **R** the veins do not separate but continue distally as a single vein. The proximal part of **M**, often known as the hamus, is absent in tingids. It is probably lost rather than fused to **Cu** since various other Heteroptera show all degrees of reduction of the hamus but no tendency to fuse with **Cu** basally.

Our conception of the venation of the cubital-anal field of the heteropteran hind wing follows that of Davis (unpublished). Just behind the cubitus there is a bifid cubital furrow (**CF**) characteristic of many Heteroptera. In tingids this furrow branches very near the base of the wing and the sector they form contains two veins which usually meet basally. The homologies of these veins in Heteroptera is uncertain and so they may be provisionally called the secondary veins (**SV**), following the terminology of Tanaka (1926). Behind the cubital furrow there is a pair of veins which are fused basally but strongly divergent distally. The anterior

18

branch is the postcubitus (**Pc**) and the posterior, the 1st anal vein (**1A**).

In some Cantacaderinae (such as the Genus *Stenocader*) there is a very small anal lobe but in other tingids the anal lobe is entirely lost.

Pregenital Abdomen. All of the abdominal segments may be distinguished although, as is generally the case in Heteroptera, the first, tenth, and eleventh segments are greatly reduced (figs. 3, 4, 5, 6). The margin of the connexivum is sharply differentiated, the ventral connexival suture is always absent, and the dorsal connexival suture is usually present but is absent in some genera of Tinginae.

Fusion of the ventral abdominal segments occurs between two and three in the Cantataderinae (fig. 6), two through four in the Tinginae (fig. 4), and two through five in the Vianaidinae (fig. 5). The remaining segments are free in all of the subfamilies. The spiracles in the Tingidae are absent on segment one; the succeeding spiracles, those of segments two through eight, are located just beneath the margin of the connexivum (fig. 6, **Sp**).

Not more than two of the three abdominal scent glands of the Heteroptera are present in Tingidae. In the Tinginae and Cantacaderinae they are median, unpaired, and placed on the anterior margin of the fourth and fifth terga. In the Vianaidinae only the scent gland of the fourth segment is present and it has widely separated orifices with unique channels extending laterad from each (fig. 27, **ASG**).

Female Genital Segments and Genitalia. In the female the seventh segment is characterized by the presence of a small median lobe which extends over the base of the ovipositor (fig. 6, **SgP**). Following the terminology used for it in other Heteroptera, this structure may be termed the subgenital plate.

The venter of the eight segment (fig. 6) is divided mesally into two sclerites each of which consists of the fused eighth paratergite (**Pt 8**) and first gonocoxopodite (valvifer) (**Gcp 1**). The place where these join is indicated by an indentation and an indistinct suture externally and by a ridge internally. The posterior ventral angle of the first gonocoxopodite is characteristically produced posteriorly.

The ninth segment is also divided mid-ventrally (fig. 6. **Pt 9**). The paired ventral sclerites of this segment represent the ventrally deflected and greatly expanded ninth paratergites. These sclerites completely cover the second gonocoxopodites and ovipositor and extend posteriorly to form the hind margin of the abdomen. The sec-

19

ond gonocoxopodites (figs. 9, 10, **Gcp 2**) are rather elongate and ensheathe the ovipositor. At the posterior end of each is a sclerotized lobe which represents the third gonapophysis (**Gap 3**).

The ovipositor (fig. 9, **Ovp**) is long and modified for cutting into plant tissue. It consists laterally of the first gonapophyses (fig. 10, **Gap 1**) and medially of the second gonapophyses (**Gap 2**). The latter are fused together for about two-thirds of their length. The saber-like first gonapophyses are held to, and slide back and forth over, the second by means of a tongue-in-groove mechanism. Their edges are finely serrate, making possible the cutting action.

At its base, each of the first gonapophyses continues dorsally as a thin, rod-like strip, the inner ramus (fig. 10, **Ra 1**). This ramus extends to and joins the ramal plate which is the inflected anterior margin of the ninth paratergite (**RaP**). The outer ramus, the skeletal component which joins the first gonapophysis to its gonocoxopodite in many Heteroptera, is lost in tingids. The first gonapophyses thus move independently of their gonocoxopodites. The second gonapophyses are each joined to the anterior ends of their

Fig. 16. Dorsolateral aspect of phallus of *T. cardui*. **Ap,** apodeme; **BF,** basal foramen; **BP,** basal plate; **Df,** ductifer.

Fig. 17. Genital duct dissected from phallus of *T. cardui*. **EjD,** ejaculatory duct; **EnD,** endophallic diverticulum; **Ens,** endosoma.

Fig. 18. Male reproductive tract of *Corythuca pallipes* Parshley. **EjB,** ejaculatory bulb; **Ms,** mesadenia; **SmV,** seminal vesicles; **Ts,** testis; **VD,** vas deferens.

Fig. 19. Dorsolateral view of phallus of *C. quadricornis*. **a,** dorsal phallic sclerite; **Ap,** apodeme; **BF,** basal foramen; **BP,** basal plate.

Fig. 20. Genital duct dissected from phallus of *C. quadricornis*. **EjD,** ejaculatory duct; **EnD,** endophallic diverticulum; **Ens,** endosoma.

Fig. 21. Male reproductive tract of *Anommatocoris coleoptratus*. **EjB,** ejaculatory bulb; **EjD,** ejaculatory duct; **Ms,** mesadenia; **SmV,** seminal vesicle; **Ts,** testis; **VD,** vas deferens.

Fig. 22. Genital duct dissected from phallus of *A. coleoptratus*. **EjD,** ejaculatory duct; **EnD,** endophallic diverticulum; **Ens,** endosoma.

Fig. 23. Dorsolateral aspects of phallus of *A. coleoptratus*. **Ap,** apodeme; **BF,** basal foramen; **BP,** basal plate.

Fig. 24. Genital chamber of *C. quadricornis*. **GCh,** genital chamber; **OdC,** common oviduct; **OdL,** lateral oviduct.
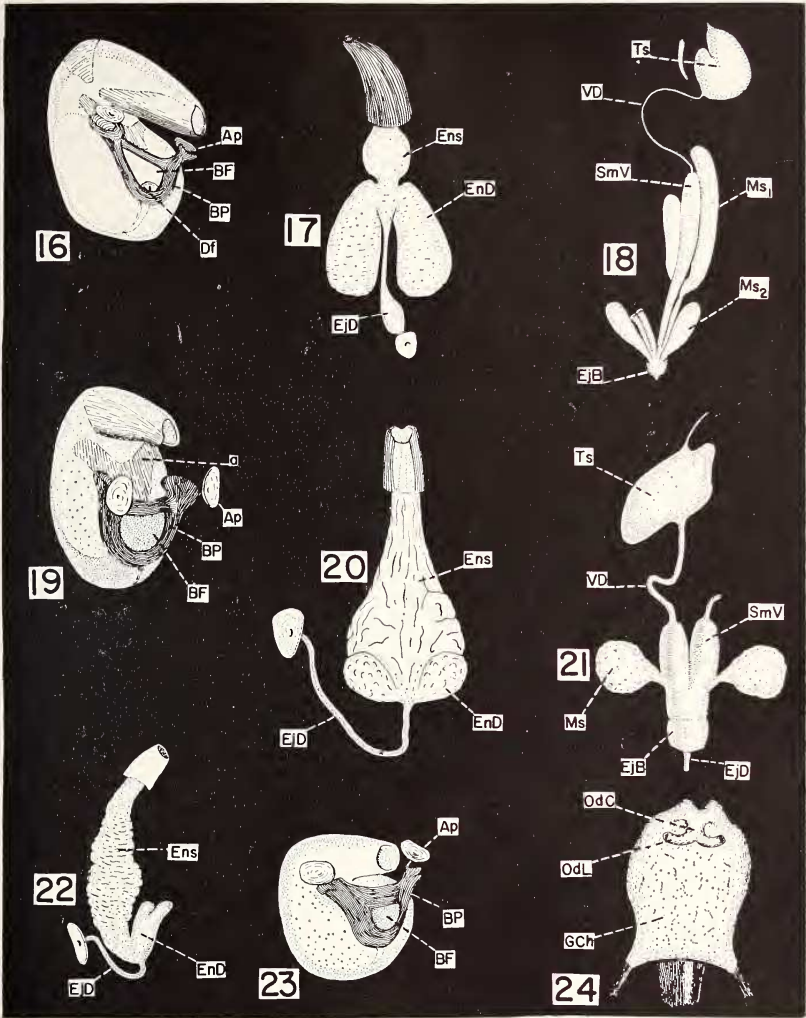
gonocoxopodites by short rami (**Ra 2**). The second gonocoxopo-
dites are articulated to the ventral ends of the ramal plates. The
musculature and mechanics of oviposition in tingids is probably
essentially identical to that described in the mirids by Davis (1955).

Internally at the base of the ovipositor is a small, membraneous
genital chamber (fig. 12, 15, **GCh**). In its roof is often a thin
sclerotized ring which encircles an area of glandular epithelium
(fig. 15, **a**). The median vermiform gland from the genital chamber,
which is the spermatheca or colleterial gland of many Heteroptera,
is absent in the Tingidae except some Cantacaderinae in which it
is vestigal (fig. 15, **Spt**). Anteriorly the genital chamber continues
as a short common oviduct or gives rise to the lateral oviducts. The
basal portion of each lateral oviduct is ectodermal, as evidenced by
a cuticular intima, and is therefore probably derived from the
common oviduct. Near their base a sac-like diverticulum extends,
from each lateral oviduct in the Tinginae (fig. 12, **SS**). Carayon
(1954) has shown that this structure functions as a sperm-receiving
organ and terms it the *saccus seminalis*, or sperm sac. These organs
are not homologous to the spermatheca of most Heteroptera but may
possibly have a common origin with the ectodermal sperm storage
organs of certain cimicomorphs such as the mirids and reduviids.

In the Vianaidinae (*Anommatocoris coleoptratus*) there appears
to be no spermathecal organ of any kind and the spermatozoa ac-
cumulate in the lateral oviducts. In the Cantacaderinae there are
no ectodermal spermathecal organs but in *Cantacader quinqueco-
status*, the only form in which we have been able to examine pre-
served material of this subfamily, there is a short curled spermathe-
cal organ situated laterally on each lateral oviduct (fig. 25, **a**).
Examination shows that this organ lacks a cuticular intima and
thus is probably mesodermal. It is clearly not homologous to the
ectodermal seminal sac of the Tinginae. It should also be noted
that *Cantacader quinquecostatus* (Fieber) has a dorsal sac which
opens broadly into the anterior end of the genital chamber (**b**).
The function of this structure is unknown but it may serve to tem-
porarily receive the spermatozoa like similar organs in the Miridae.

The number of ovarioles comprising the ovary is reported to be
7 in the Tinginae (Carayon, 1950b) and in the Cantacaderinae (*C.
quinquecostatus*) there are 5 ovarioles (fig. 25, **Ov**). The number
in the Vianaidinae is unknown at present.

Male Genital Segments and Genitalia. The eighth segment is
not markedly reduced as it is in a number of Heteroptera. The
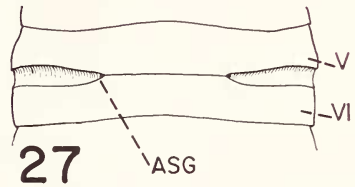ninth segment, or pygophore, (figs. 3, 11, **Pg**) is not deeply tele-
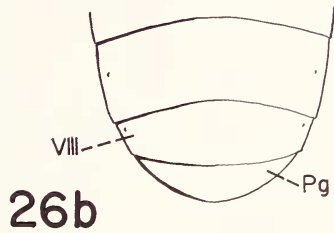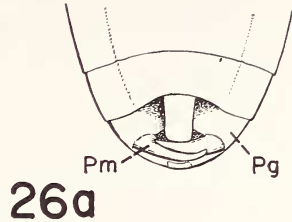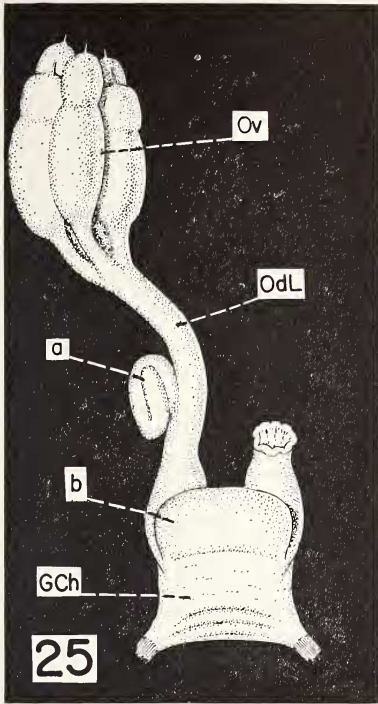
Fig. 25.   Female reproductive tract of *C. quinquecostatus*. a, spermathecal organ; b, dorsal sac; GCh, genital chamber; OdL, lateral oviduct; Ov, ovary.

Fig. 26a.   Dorsal aspect of terminal genital segments of *A. coleoptratus* male. Pg, pygophore; Pm, parameres.

Fig. 26b.   Terminal abdominal segments of *A. coleoptratus* male. Pg, pygophore; VIII, eighth abdominal segment.

27.   Dorsal abdominal scent glands of *A. coleoptratus* nymph. ASG, abdominal scent gland; V–VI, fifth and sixth abdominal segments.

scoped into the rest of the abdomen and therefore it is exposed dorsally. On its posterior dorsal surface it bears a distinct quadrate sclerite which represents the tenth segment (**Pgr**). As in other Heteroptera this segment bears the anus and is therefore termed the proctiger.

On each side of the proctiger the genital claspers, or parameres, extend from the pygophore (fig. 3, **Pm**). They are typically simple, curved, thick basally, and gradually narrow to a more or less pointed apex. At rest, they lie folded over one another across the posterior rim of the pygophore.

The structural characteristics of the tingid phallus are remarkably uniform and only minor differences are found even between the subfamilies. In shape the phallus is characterized by a broad, thick basal region which tapers apically to a more slender tubular portion that curves back over the base (figs. 16, 20, 23). On the proximal end is a distinct, stirrup-shaped sclerite (fig. 16, **BP**) characteristic of the heteropteran phallus generally and known as the basal plate. The arms of this sclerite serve to articulate the phallus to the suspensory arms (fig. 8, **SAr**) of the pygophore on which the phallus swings out from or into the genital chamber. These movements are produced by muscles inserted on apodemes (fig. 16, **Ap**) arising from the basal plate. On the dorsal surface of the phallus, just anterior to the basal plate, there is a more or less distinct ''Y''-shaped sclerite whose arms extend anteriorly and laterally (Fig. 19, **a**). The apex of the phallus is also surrounded by a sclerotized region but other than this and the sclerites described above, the wall of the phallus is largely membraneous.

The basal plate circumscribes a broad opening, the basal foramen (fig. 16, **BF**) into the phallus. At the ventral edge of the basal foramen there is often a small sclerotized bridge, the ductifier (**Df**) through which the ejaculatory duct (fig. 17, **EjD**) passes into the phallus. Within the phallus the duct enlarges into a broader and somewhat wrinkled passage which is the endosoma (fig. 17, **Ens**), and at the base of the endosoma there is a paired or median (Vianaidinae) diverticulum (**EnD**). These unique structures of the tingid phallus were first noted by Singh-Pruthi (1925); nothing is known of their function but they are presumably reservoirs for the semen and may also be involved in some way in the erection of the endosoma.

The endosoma, however, can be everted only relatively little. It may be further characterized by its lack of appendages and, as is characteristic of other cimicomorphs, it is not differentiated into vesica and conjunctiva.
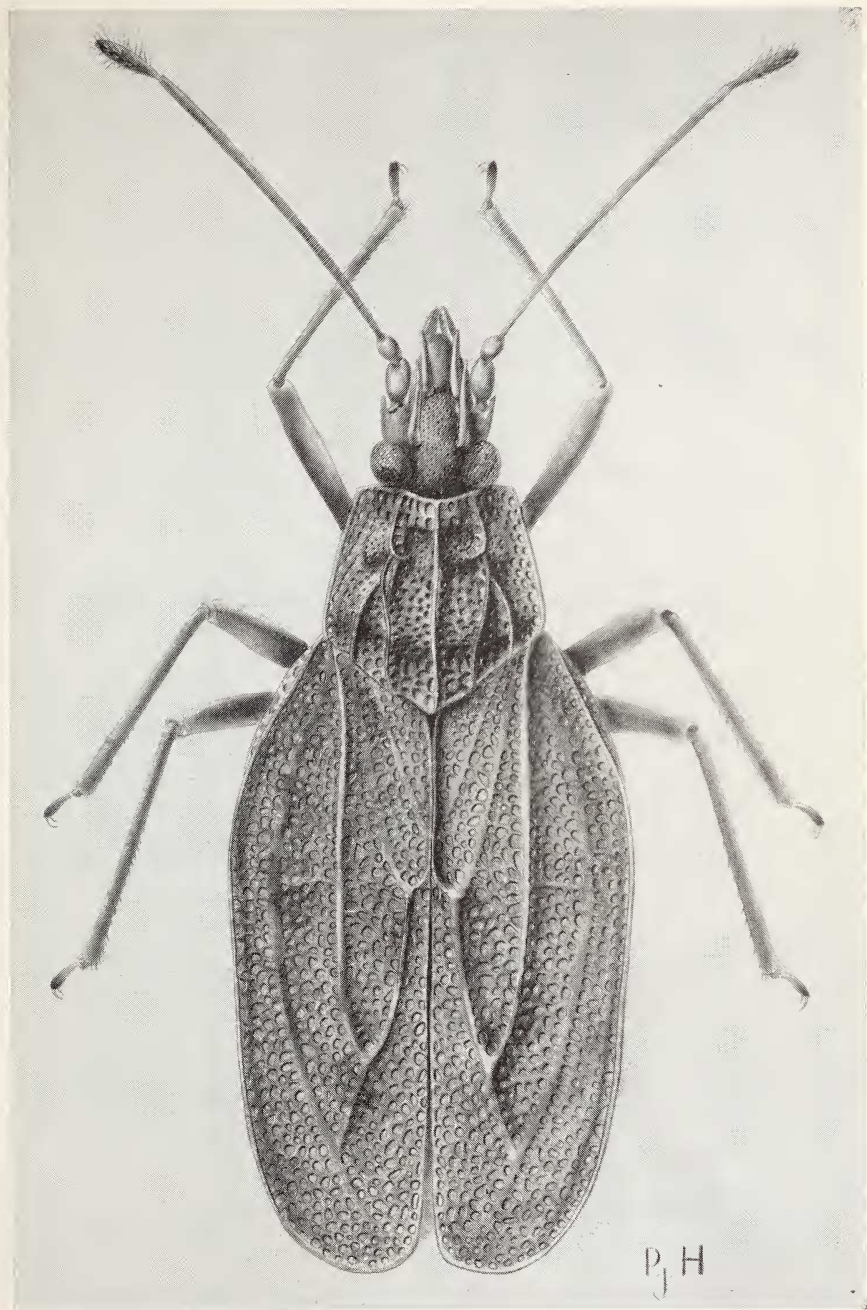
Fig. 28.   *Cantacader quadricornis* (Le Peletier and Serville).
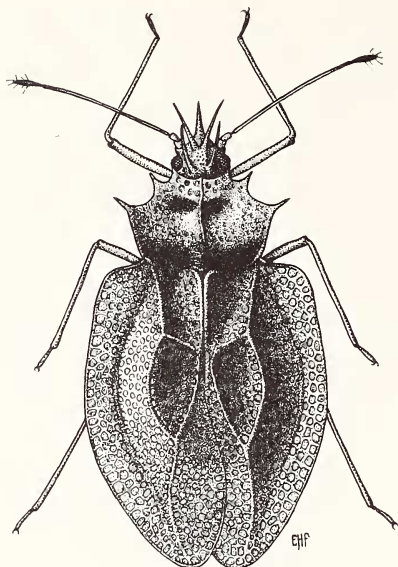
Fig. 29.   *Oranoma biroi* Drake.

The proximal end of the ejaculatory duct does not extend from the phallus as it does in many heteropterons but instead joins the mesodermal portion of the male reproductive tract right at the basal foramen. This latter portion of the tract has been studied in several Tinginae and in one alcohol-preserved specimen of a vianaidine (*Anommatocoris coleoptratus*). In the Tinginae the testes are generally globular (fig. 18, **Ts**) and their follicles are indistinct; leading from each is a slender vas deferens (**VD**) the distal portion of which enlarges to form the seminal vesicle (**SmVs**) along side of which there is an elongate tubular accessory gland, the mesadene (**Ms₁**). Basally the mesadenia and seminal vesicles merge into a median structure, the ejaculatory bulb (**EjB**), which in turn is joined to the ejaculatory duct at the basal foramen of the phallus. Arising dorsally from the seminal pump is a small second pair of accessory glands (**MS₂**); these simple diverticula have been designated as ectadenia (viz., ectodermal accessory glands) by Pendergast (1957) but since they lack a cuticular intima, they are probably of mesodermal origin and therefore may constitute an additional pair of mesadenia.

In the Vianaidinae (*A. coleoptratus*) the seminal vesicles (fig. 21, **SmV**) are short, thick, and partly incorporated into the ejacu-

Fig. 30. *Ceratocader armatus* (Hacker).

latory bulb (**EjB**); there is a single pair of mesadenia (**Ms**) and these are globose. The male reproductive system of the cantacaderine, *C. quinquecostatus,* possesses a large and small pair of tubular mesadenia and long tubular seminal vesicles and is thus very similar to the male reproductive system of the tingines.

FAMILY RELATIONSHIPS OF THE CIMICOMORPHA

In the past various authors (Reuter, 1910, 1912; China, 1933; Börner, 1934) have considered the Tingidae to be related to the Piesmatidae and have placed them with those families of Geocorisae which are now often designated as the Pentatomomorpha rather than with the other major division of the Geocorisae, the Cimicomorpha (*in sensu* Leston, Pendergrast, and Southwood, 1954). However, Tullgren as early as 1918 pointed out that the tingids, unlike the Piesmatidae and related families, lack ventral trichobothria and he therefore concluded that the tingids are unrelated to the piesmatids. Singh-Pruthi (1925), although failing to recognize this lack of relationship, demonstrated that the tingid phallus is of the reduvioid (= cimicomorph) type. Leston *et al* (1954) gave additional evidence concerning the relationships of the Tingidae and formally placed them in the Cimicomorpha. Tingids have the following characteristics of this group: Ventral trichobothria absent, hind wing with vein RM distally fused and subcosta distinct, true spermatheca absent; phallus with endosoma not differentiated into vesica and conjuctiva and eggs with a well differentiated operculum.

Although the tingids clearly belong to the Cimicomorpha, their relationships to other members of this group are very poorly known. Leston *et al* (1954) and Pendergrast (1957) suggest that existence of paired pseudospermathecae in tingids and reduviids indicates a relationship between these families. Previously Carayon (1954) had noted the similarity of the tingid pseudospermathecae to the corresponding organ of the mirids; in the tingid Genus *Kapiriella,* however, he found the organs to be like those of the reduviids and therefore concluded that the phylogenetic position of the tingids is between the mirids and reduviids. China (1955) in a recent consideration of heteropteran phylogeny also relates the tingids to the Reduvioidea and suggests a very early divergence from the reduviid and joppeicid line.

Determination of the phylogenetic position of the Tingidae is made especially difficult by the particularly complex and often poorly known relationships of the other cimicomorph families. Two

Fig. 31. *Cyperobia correctorum* Bergroth.

superfamilies, the Reduvioidea and Cimicoidea, established by
Reuter (1910) are customarily recognized in the Cimicomorpha.
The Reduvioidea as defined by Reuter are distinguished from the
Cimicoidea by their simple meso- and metasterna, rotatory meta-
coxae, and symmetrical male genitalia.   In contrast the Cimicoidea
have composite meso- and metasterna, cardinate metacoxae, and
asymmetrical male genitalia.   The distinction between the two
superfamilies on the basis of these characteristics have, for the most
part, long since been invalidated and the superfamilies have not
been clearly redefined.   This invalidation has come in part from a
recognition of exceptions to definitions of the respective superfami-
lies.

China and Myers (1929), for example, point out that the Microphysidae, although in Cimicoidea, have symmetrical genitalia, and McAtee and Malloch (1925) have shown that the meso- and metasterna characters are of questionable value in phylogeny. Further invalidation of the respective superfamily definitions has come about by the placing of additional families such as Joppeicidae (China, 1955) and Tingidae in the Reduvioidea, the Thaumastocoridae (Drake and Slater, 1957) in the Cimicoidea, and the moving of the Nabidae from the Reduvioidea to the Cimicoidea (Carayon, 1950). In each of these cases the particular family concerned has characteristics contrary to those on which its respective superfamily is based.

Since the superfamily categories of the Cimicomorpha are in such an unsettled state at present, it will be more convenient to discuss the affinities of the Tingidae on the basis of individual families or certain groups of distinctly related families. The reduvioid families constitute one such group. In discussing the status of the Reduvioidea Davis (1957) has pointed out that of the various families that from time to time have been assigned to this group, only the Phymatidae, Elasmodemidae, and Pachynomidae are clearly related to the Reduviidae. Carayon, Usinger, and Wygodzinsky (1958) have subsequently concluded that the phymatids and elasmodemids are in fact so close to the reduviids that they should be reduced to the rank of subfamilies of the Reduviidae.

The Microphysidae, Anthocoridae, Cimicidae, and Polyctenidae have long been recognized as closely allied families and this relationship has been well substantiated by the extensive studies of Carayon. In addition Carayon (1950) has shown that the Nabidae are more closely related to these families than to the Reduviidae as was generally held previously. Blöte (1945) has pointed out that *Velocipeda biguttata* Reuter is a synonym of *Scotomedes ater* Stål and that Stål was correct in placing this group in the Nabidae. He therefore has lowered the family Velocipedidae to the subfamily level and placed it in the Nabidae under the name Scotomedinae. China and Miller (1955) note that the familial name, Velocipedidae Bergroth, has priority and feel that although closely allied to the Nabidae, it represents a distinct family.

The Isometopidae are generally placed very close to the Miridae and Carayon (1958) has recently presented evidence which he feels indicates that the isometopids should be treated as a subfamily of the Miridae. The mirids are known to have certain affinities with the previous group of families but are nevertheless distinctly removed from them.
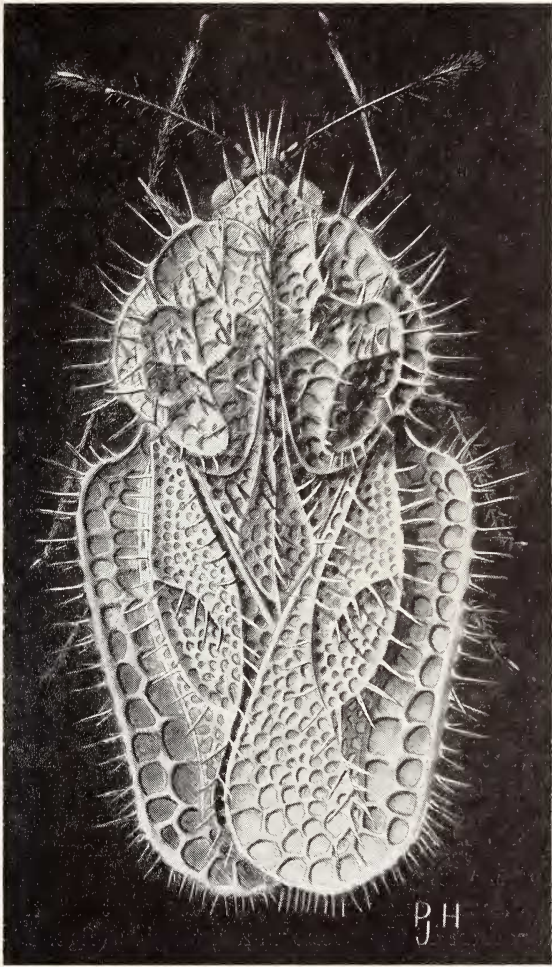
30

Fig. 32. *Urentius echinus* Distant.

As noted previously the position of the Tingidae in the Cimico-morpha has not yet been clearly established. However, Kormilev (1955) in describing the family Vianaididae as a small group of myrmecophilous bugs, shows that they are relatives of the Tingidae, and in the present paper it is concluded that these insects should be placed as a subfamily of the Tingidae.

In concluding this survey of the Cimicomorpha we may note that Drake and Slater (1957) place the Thaumastocoridae with the cimicoid families but indicate they have certain reduvioid charac-teristics; conversely China (1955) places the Joppeicidae closest to the reduvioids but finds that they have certain similarities to the Nabidae and Anthocoridae.

Phylogenetic Characters of Tingidae and other Cimicomorpha

The tingid head in its combined characteristics resembles most that of the Miridae. And, as in that family, the head is inserted into the pronotum up to the eyes, is usually declivent (although often less so than the mirids), has well developed bucculae, the first segment of the beak is not reduced and, like the Miridae (except in the Isometopinae), the ocelli are absent. Taken individually, these points of similarity between the tingid and mirid head are not of much importance but collectively they appear to be significant. The reduvioids differ from the tingids in having a more elongate head, eyes separated from the pronotum, ocelli usually present, bucculae absent, and a beak that is usually thick, curved, and apparently three-segmented. The cimicoid head differs from that of the tingids in usually being porrect, having ocelli, lacking bucculae, and having the first segment of the beak greatly reduced or indistinguishable. The antennae of tingids bear no strong resemblance to those of other cimicomorphs except perhaps the Joppeicidae in which, like many tingids, the first two segments are generally short and the third almost always the longest.

The pronounced and assorted development of the paranota, carinae, and collum of the pronotum of tingids (figs. 30, 31, 45, 55, 59) is without similarities in other families of Cimicomorpha and apparently of no value in the phylogeny of the family. Since these developments are often more pronounced in the most highly evolved subfamily, the Tinginae (figs. 37, 43, 44, 71), they probably evolved after the family became a distinct unit.

Much use in heteropteran phylogeny has been made of the two types of metacoxae, cardinate and rotatory, as described by Schiödte

(1870). The cardinate type is characterized by its relative lack of mobility, this being limited to slight back and forth movements. The elongate coxa lies in a large coxal cavity and its dorsal articulation is near the upper edge of the pleuron. The epimeron and sternum are said to be reduced. The second type, the rotatory coxa, is characterized by relatively free movements of partial rotation around its longitudinal axis, and the coxa is shorter, more cylindrical, and fits into a socket in the lower portion of the pleuron. The epimeron and sternum are well-developed.
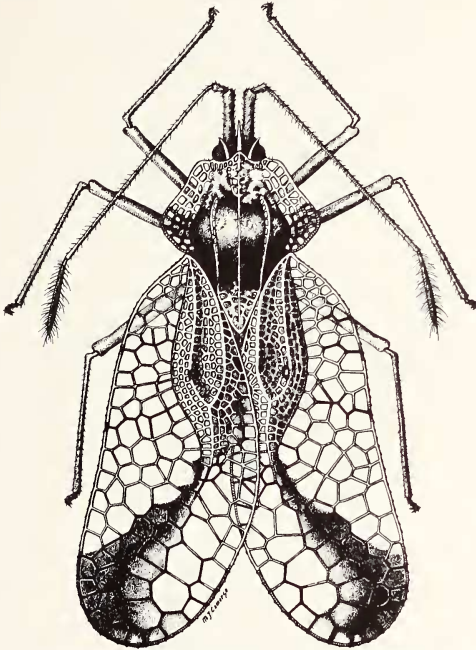
Fig. 33.   *Gargaphia obliqua* Stål.

Schiödte placed great phylogenetic importance on these coxal types and on the basis of them divided the families of Heteroptera into two major groups. The families of Cimicoidea and some of the aquatic families comprised the group with cardinate coxae and were termed the Pagiopoda ; those with rotary coxae, the pentatomomorph families, the reduvioid families, and the remainder of the aquatic families, were placed in a second group, the Trochalopoda. These systematic categories did not find lasting acceptance but the two types of coxae, as described by Schiödte, have frequently been

33

used by systematatists to characterize various other higher categories.

Actually the two types of coxal articulations are not as fundamentally different from each other as Schiödte indicated. Insects that have coxae that are truly cardinate, or hinged, have a dicondylic joint whose movement is thus fixed about a single axis. In typical pagiopodous heteropterons, however, the coxa is articulated to the pleuron but not to the sternum and is therefore monocondylic.
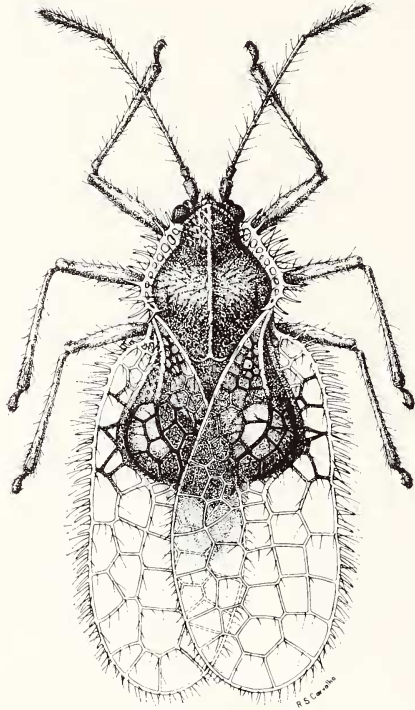

Fig. 34. *Acanthocheila visenda* Drake and Hambleton.

Its movements are not fixed about a single axis but normally the coxa rotates partially about its own longitudinal axis. The coxa is diagonal to the frontal plane of the body and converges with its opposite member. Since the coxa is turned under, its rotation moves the trochanter back and forth and it may therefore superficially appear to be hinged.

34
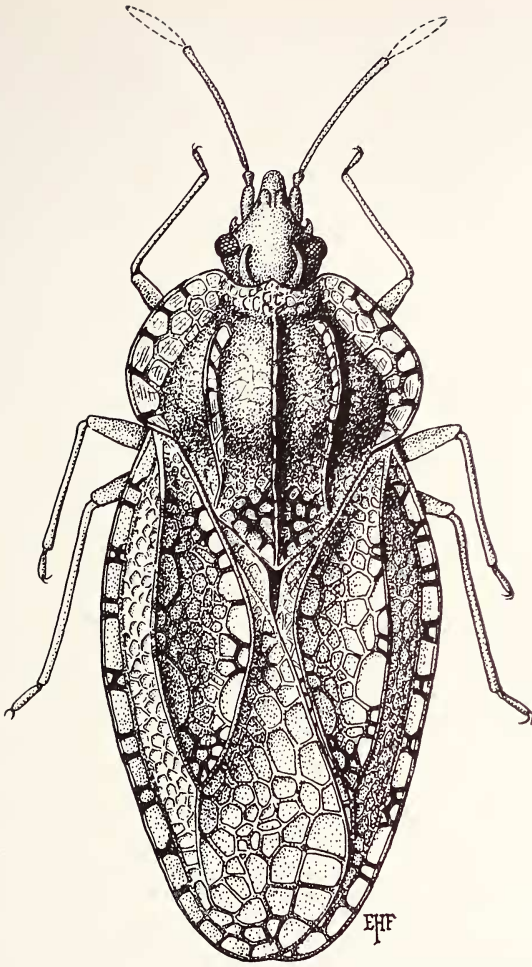
Fig. 35. *Dictyonota pakistana* Drake and Maldonado.

In the typical trochalopodous heteropterans the coxa is also monocondylic but is more nearly perpendicular to the frontal plane and adapted to rotate through a broader arc. The sternum and episternum often project around the base of the coxa forming a socket which limits the coxa to rotatory movements. Since the episternum extends over the base of the coxa its pleural articulation is concealed and the coxa appears to be shorter than it actually is.

35

The so-called cardinate coxa, no doubt, represents the primitive form and the rotatory type has evolved from it. Since the rotatory coxa is found in such unrelated families as the Reduviidae, Gerridae, and Pentatomidae, it seems likely that it has evolved independently in several instances. Furthermore, in some cases the coxa may be considered to be intermediate between the so-called cardinate and rotatory types. In *Leotichius,* China (1933) has designated the hind coxa as semipagiopodous. The hind coxa of nabids is also of this type.

From the foregoing considerations we may draw these conclusions: Although many families of Heteroptera can be characterized as having either the so-called cardinate coxa or as having rotatory coxa, there is actually no clearly distinct dividing line between the two types and some families have an intermediate type. Since apparently the rotatory type has evolved independently in several families, caution must be exercised in the use of this character as evidence of a relationship between families. However, the structure of the metacoxa in any given group can be used along with the other characters of a similar nature to evaluate the relative primitiveness of the group.

In the tingids the hind coxa is a fairly advanced rotatory type but not as highly evolved as that of the reduvioids. Rotatory coxae are also found in the Thaumastocoridae and as mentioned above the hind coxae of nabids are intermediate between the rotatory and cardinate types. The remainder of the cimicomorphs have the more primitive cardinate type coxae.

The reduction of the tarsus of tingids to two segments occurs also in several other cimicomorph families and in some families both the two- and three-segmented condition is found. Since the reduction of the tarsal segments appears to have occurred independently in a number of cases, it is of little value as a phylogenetic character at the familial level. Arolia and pseudoarolia occur in the mirids and some Thaumastocoridae but not in the tingids and other cimicomorphs. However, the peculiar tooth found at the base of the tingid claw is remarkably like that found in the mirid Subfamily Deraeocorinae.

The metathoracic scent gland apparatus of tingids resembles that of the Reduviidae and Pachynomidae in that it has paired rather than a median reservoir as in other cimicomorphs. As noted above the paired condition probably is a specialization resulting from the reduction and eventual loss of the median portion of the reservoir. Since several other families of Cimicomorpha have a

deeply bilobed median reservoir suggestive of an intermediate condition leading to the development of paired reservoirs, it is quite possible that the paired condition could have developed independently in the tingids and in the reduvioids. Furthermore, the paired condition of the scent gland reservoir occurs in the Aradidae and Pyrrhocoridae of the Pentatomomorpha (Carayon, 1955) and
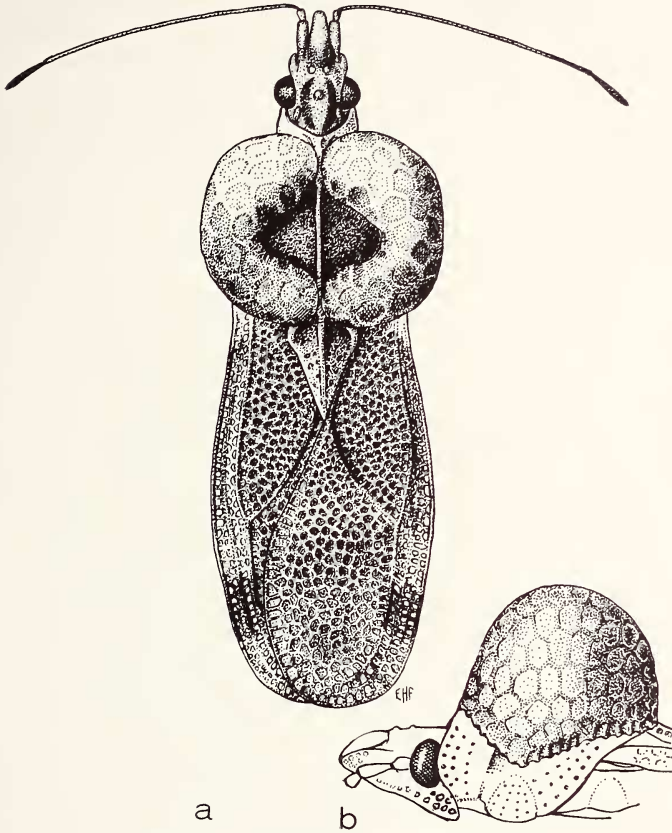

Fig. 36. *Ypsotingis bakeri* Drake
a, Dorsal; *b*, Lateral

therefore has also apparently evolved independently of both the tingids and the reduviids.

The scent gland apparatus of reduviids is considerably more reduced than that of the tingids and it is frequently absent. In the forms in which it is moderately well developed, such as in *Melano-*
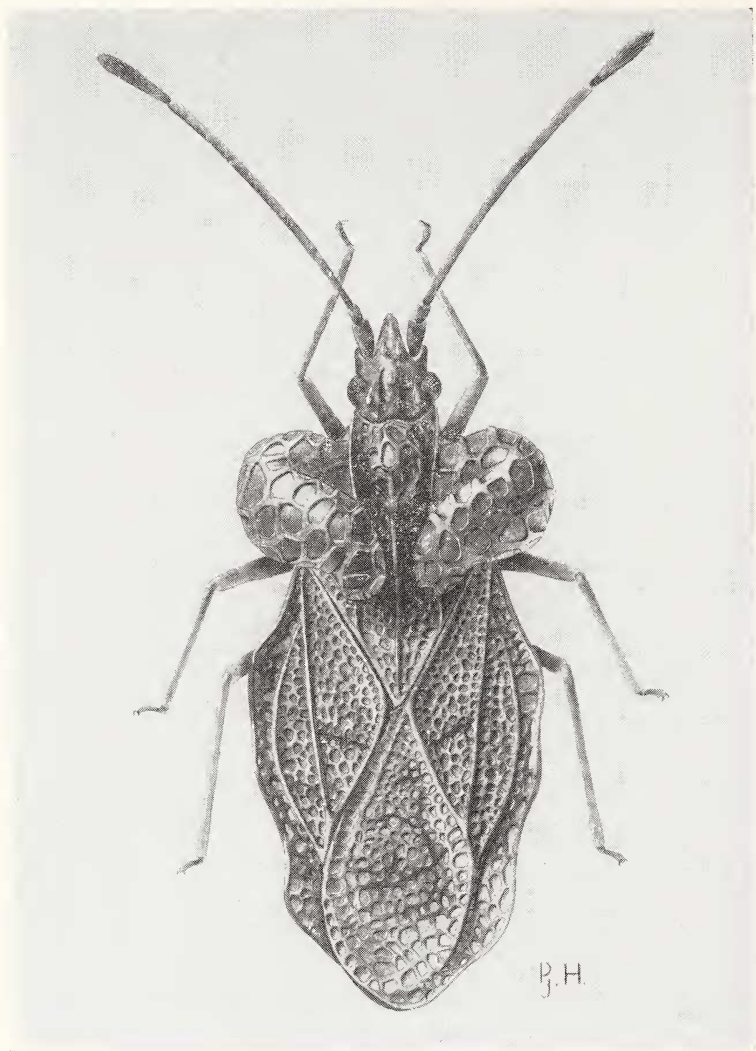
Fig. 37.   *Dictyotingis gibberis* Drake.

lestes picipes (H.S.), each reservoir has a tubular gland appended to its base. Such a gland is not found in the tingids, and the secretion is apparently produced by a glandular epithelium on the wall of the reservoir. Externally, the scent glands of reduviids show a great reduction of the scent gland apparatus in the loss of the pleural ostiole; each gland opens into an inconspicuous groove along
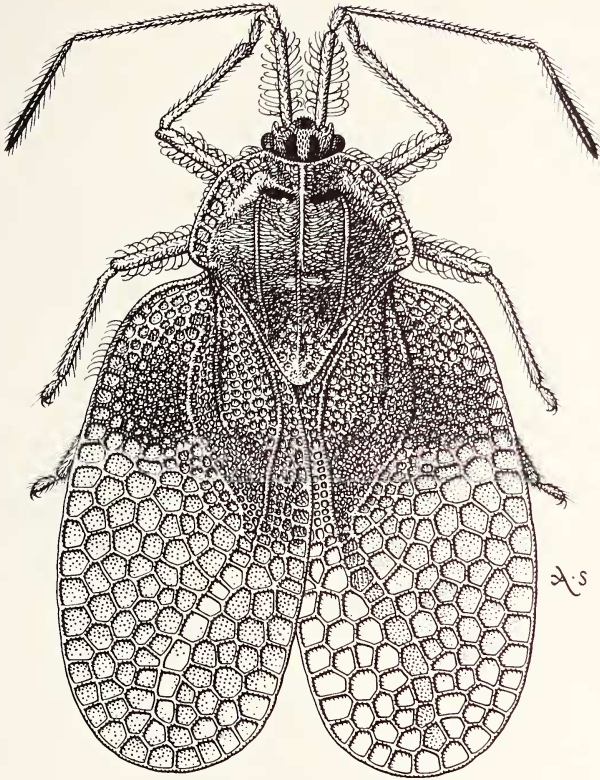

Fig. 38. *Nobarnus signatus* Distant.

the anterior margin of the coxal cavity. In contrast the pleural ostioles of tingids are usually present, although they are not as prominent as in many other cimicomorphs.

In addition to the usual metathoracic scent glands, many reduviids have a second pair of glands, called Brindley's glands, which open near the upper posterior corner of the metepimeron.
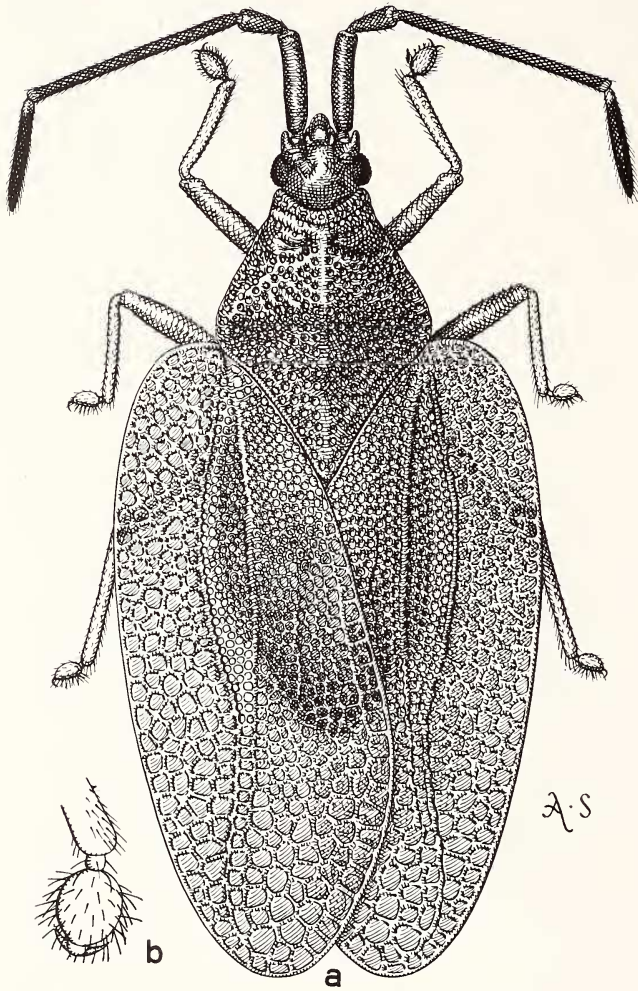
Fig. 39. *Litadea delicatula* China.

Since the scent glands of the Tinginae are often attached to the thorax in nearly the same position, they resemble Brindley's glands. However, their connection to the pleural ostiole and their position in the cantacaderines clearly indicate that they are not homologous to Brindley's glands but to the metathoracic scent glands of the Heteroptera.

Externally the reduvioids show a further reduction of the scent gland apparatus in the loss of the pleural ostioles; each gland opens
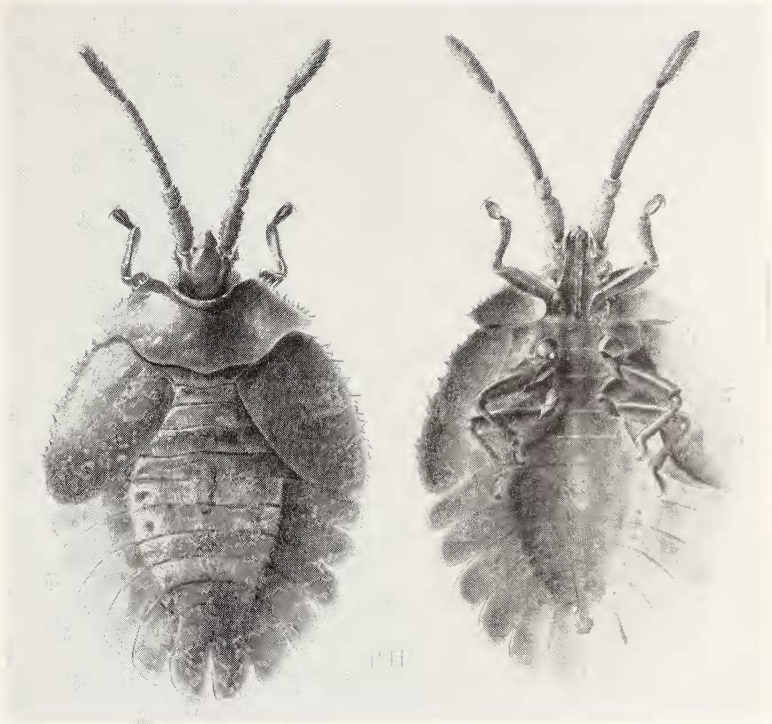
Fig. 40. *Litadea delicatula* China, (nymphs) **a**, dorsal and **b**, ventral aspects.

into an inconspicuous groove along the anterior margin of the coxal cavity. The pleural ostioles of the tingid glands are present although not as prominent as in many other cimicomorphs.

The features of lacy ornation of the hemelytra like those of the pronotum appear to be of little phylogenetic significance at the family level. The development of a hypocosta and expanded costal area of tingids, as we have noted, is similar to the condition of cer-

41

tain mirids and velocipedids and is quite unlike the nabids and reduvioids.

The characteristic lack of the hamus in the tingid metathoracic wing is shared with very many of the other families or subfamilies of the Cimicomorpha but not with most Reduviidae nor with nabids of the subfamilies Prostemminae and Nabinae. On the other hand, the development of the intercubital area resembles that of the Re-
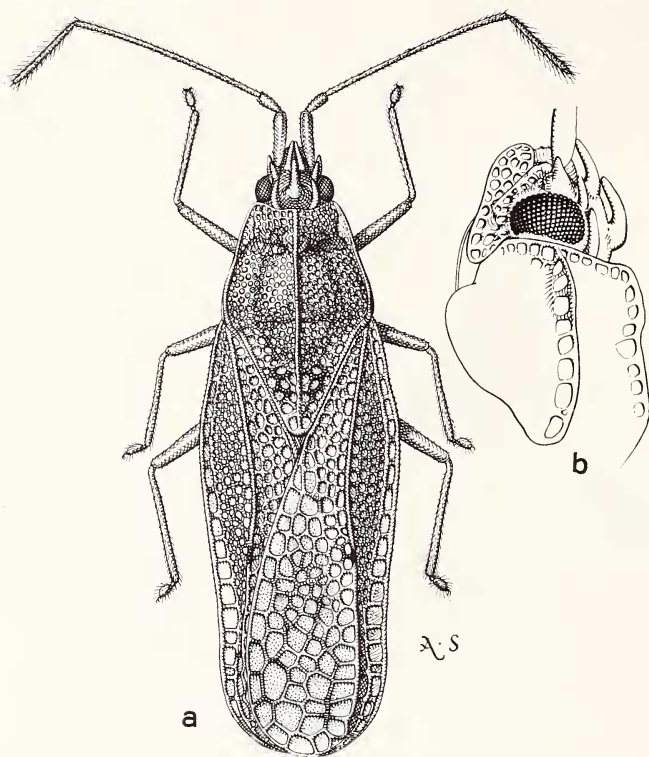

Fig. 41. *Orygotingis insularis* (China), **a**, dorsal aspect; **b**, profile of head and thorax.

duviidae in which two veins are usually present and joined proximally. Other Cimicomorpha usually show some reduction of the intercubital area and veins; in mirids and nabids of the subfamilies Prostemminae and Nabinae, and in at least some anthocorids there is usually only one intercubital vein. In Joppeicidae and Isometopinae and Velocipedinae the intercubital area lacks veins and the

intercubital area itself is lacking in Thaumastocoridae, in the nabid Genus *Arachnocoris,* and in at least some Microphysidae.

The basally fused and distally divergent condition of the **Pc** and **1st A** in tingids is also characteristic of the condition in many nabids, anthocorids, mirids, and at least some isometopids and microphysids (*Mallochiola,* McAtee and Malloch, 1924). In another microphysid (*Plokiophilia,* China and Meyer, 1929, p. 111, fig. **d**), and in Thaumastocoridae (Drake and Slater, 1957, p. 355, fig. 17) and Joppeicidae (China, 1955, p. 355, fig. **d**) only the postcubitus
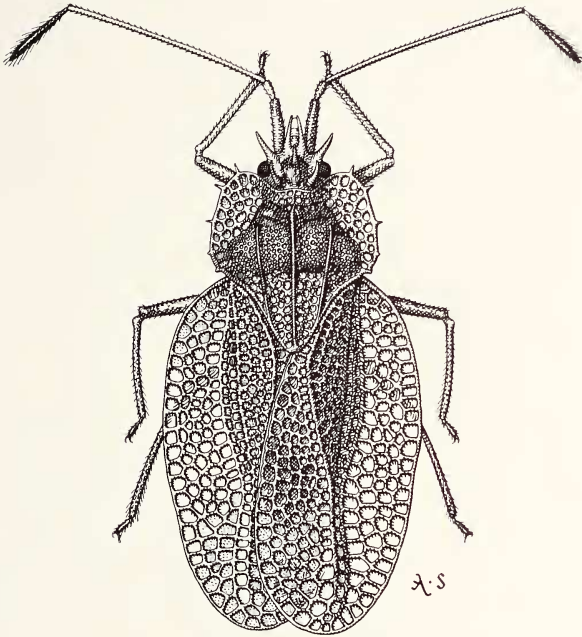
Fig. 42. *Corinthus typicus* Distant.

is present. In Reduviidae the basal fusion of **Pc** and **1st A** is not pronounced and these veins are not divergent but almost parallel.

The reduction and loss of the anal lobe probably occurred in the tingids after they became a distinct group since a very small anal lobe is found in some Cantacaderinae. However, a considerable reduction of the anal lobe is also apparent in many of the cimicomorphs, especially joppeicids and thaumastocorids. The illustrations of the hind wing of certain microphysids (China and Meyers,
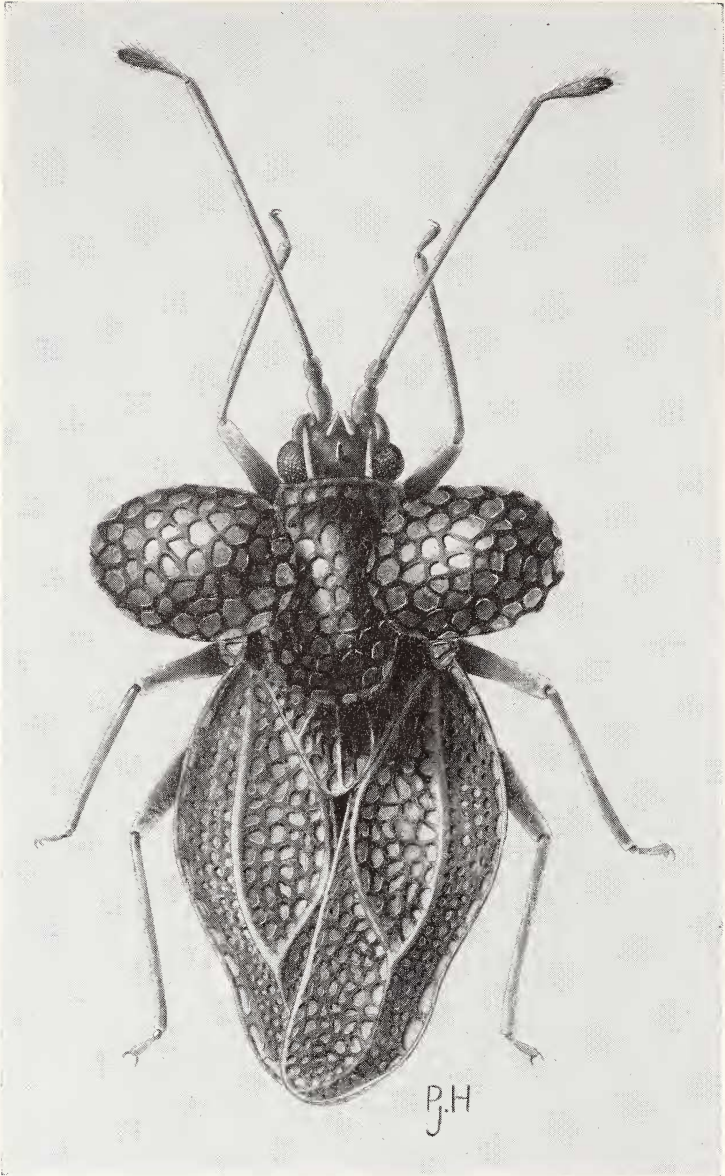
43

Fig. 43. *Diplocysta trilobata* Drake and Poor (dorsal aspect).

1929, and McAtee and Malloch, 1924) seem to show that the anal lobe is also absent.

The pattern of ventral fusion of abdominal segments of tingids is similar to that of most cimicomorphs in which only segments two and three and occasionally three and four are fused while the others are free. In the reduviids, however, all of the pregenital segments are completely fused. The reduviids, pachynomids, and nabids of

Fig. 44.   *Diplocysta trilobata* Drake and Poor (oblique view).

the Subfamily Nabinae have ventral connexival sutures, while in tingids and other cimicomorph families this suture is lacking. Carayon (1950) has pointed out that the first abdominal spiracles, which are dorsal in position, are present in the Reduviidae, Phymatidae, and Pachynomidae, but are absent in the Nabidae. Drake and Slater (1957) report that they are also present in the Thaumastocoridae. These spiracles are absent in the Tingidae and a preliminary check that we have made indicates they are also absent in the Anthocoridae, Cimicidae, and Miridae.
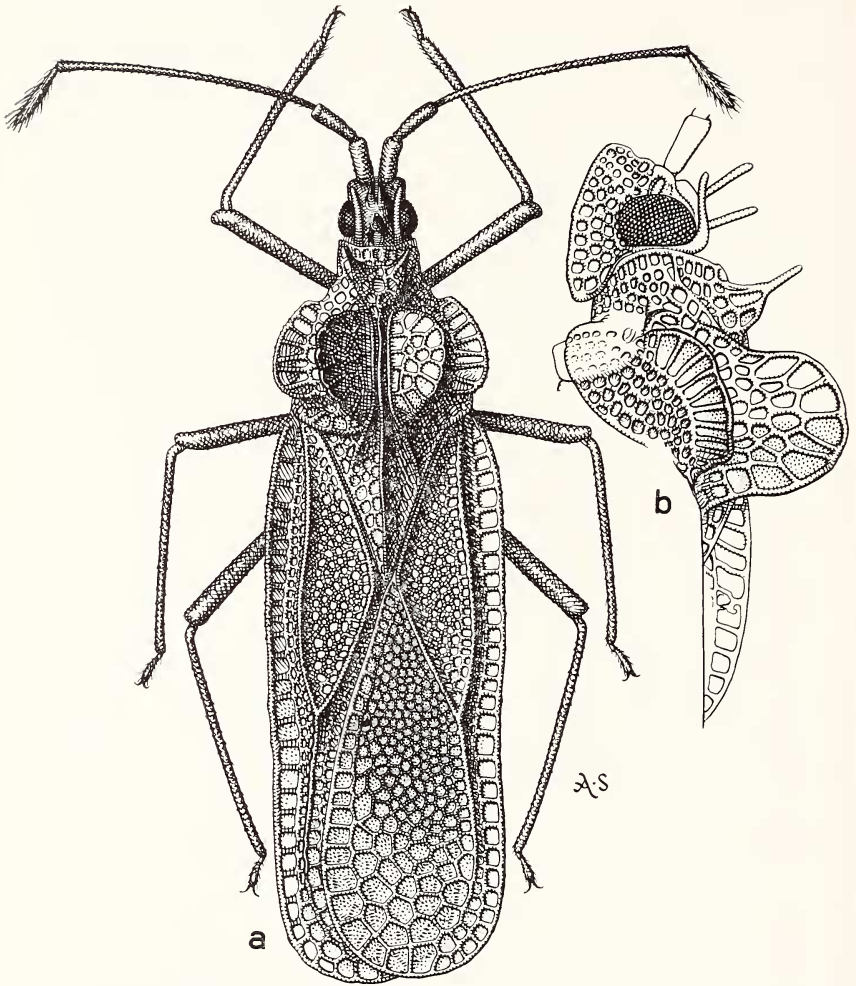
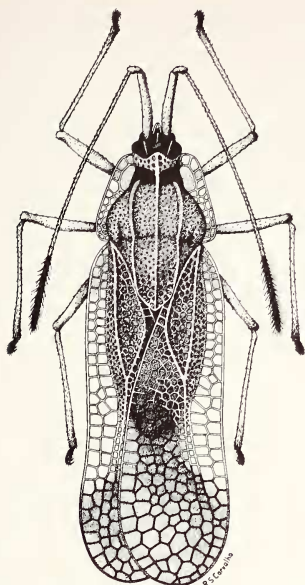Fig. 45. *Furcilliger cheesmanae* Drake, **a,** adult; **b,** lateral aspect.

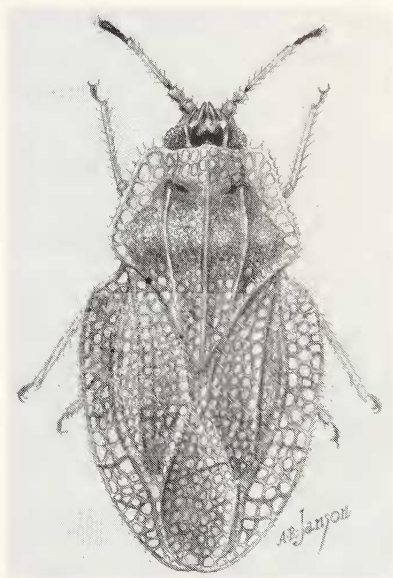Fig. 46. *Idiostyla rollinae* Drake and Hambleton.

Fig. 47. *Tingis colombiana* Drake.

The external female genitalia of cimicomorphs show all degrees of development from the long, drilling-type ovipositor of mirids, tingids, and most nabids, to the very short, stubby ovipositor of reduviids,[2] or to the complete loss of the gonapophyses in the thaumastocorids, in some nabids (Arachnocorinae), and in some microphysids (Plokiophilinae, China, 1953). China and Myers (1929) indicate that in the Anthocoridae the ovipositor varies from fully developed to completely absent, and China (1955) states that the ovipositor is also absent in Joppeicidae; however it is not clearly indicated whether the gonapophyses are completely absent or are greatly reduced.

Since within several families of Cimicomorpha well developed ovipositors are found as well as various degrees of reduction and loss of the ovipositors, this reduction and loss appears to have occurred independently in the Cimicomorpha and is of little value in interpreting family relationships. The drilling-type ovipositor has essentially the same structure in all of the families in which it is found and since it is composed of all of the basic elements of the primitive insect ovipositor, it probably represents the approximate archetype of the external female genitalia of the Cimicomorpha.

One feature of the ovipositor that appears to be of phylogenetic significance is the relationship of the first gonapophysis to its gonocoxopodite. In the primitive condition this blade of the ovipositor is attached to its gonocoxopodite by an outer ramus and to the ninth paratergite by an inner ramus; furthermore, the gonocoxopodite is separated from the eighth paratergite by a conjunctiva and is usually directly involved in the movements of the first gonapophysis. This condition is found in the anthocorids, cimicids and nabids. In mirids and tingids the ramus connecting the gonapophysis to the gonocoxopodite is lost, the gonocoxopodite is fused to the paratergite, and the gonapophysis moves independently of its coxopodite. In the tingids the first gonocoxopodite can still be distinguished but in the mirids it forms an indistinguishable part of the eighth paratergite (eighth sternum of many authors).

---

[2] It is sometimes stated that heteropterons which have short gonapophyses (such as the reduviids) lack an ovipositor and the term ovipositor is applied only to the long shaft-like organ of forms such as in the mirids, nabids, and lygaeids. This use of the term is quite undesirable since it suggests that there are two distinct conditions, absence of the ovipositor or presence; actually intermediate conditions exist. Since the gonapophyses, regardless of their development, are concerned with oviposition, they may be referred to collectively as the ovipositor.
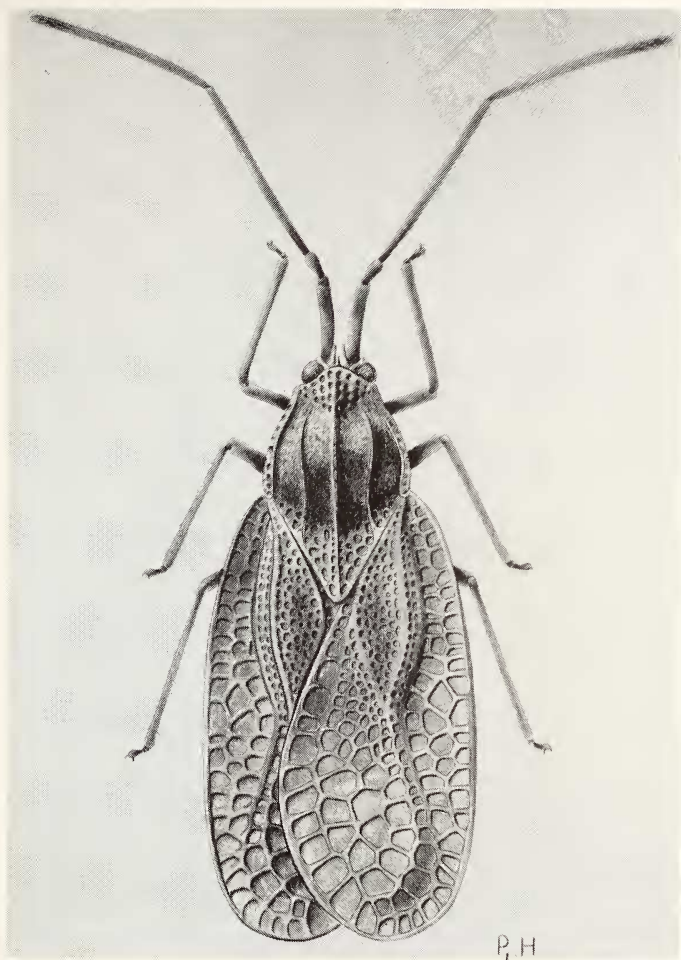
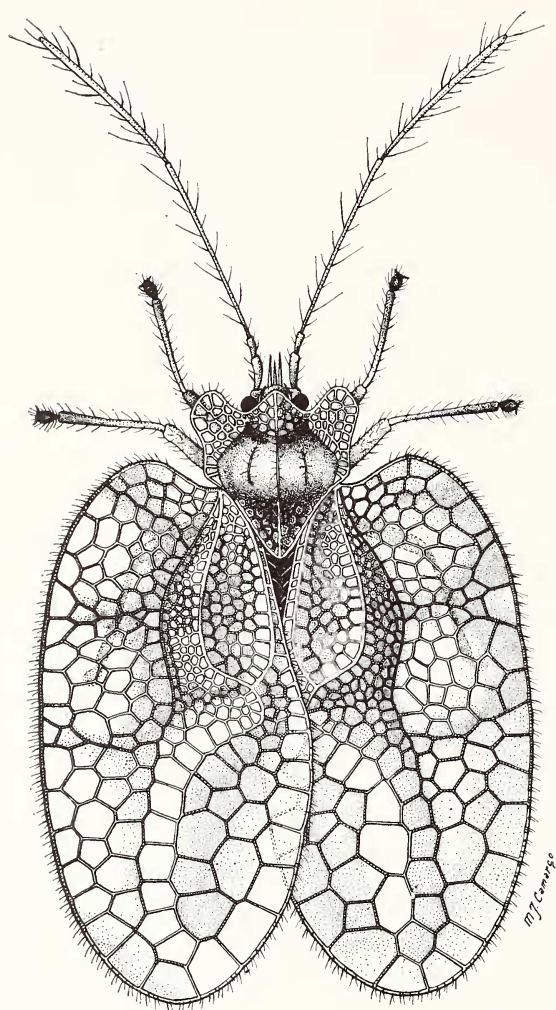Fig. 48.   *Macropharsa hackeri* Drake.

Fig. 49. *Pleseobyrsa atratarsis* Drake and Hambleton.

Reuter (1910) noted that in the Anthocoridae and Microphysidae there is a small triangular sclerite on each side of the base of the ovipositor and this sclerite is lacking in the Miridae; he uses this difference as one of the characteristics distinguishing two phalanges, the Cimiciformes and Miriformes respectively, in his superfamily Cimicoidea. This triangular sclerite is what has been identified above as the first gonocoxopodite.
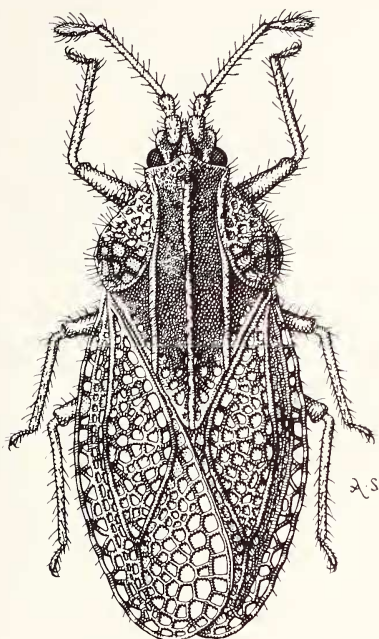

Fig. 50. *Onymochilla dichopetali* (Horváth).

In the Cimicidae (Davis, 1956) and apparently also in those anthocorids in which the ovipositor is reduced, the first gonocoxopodite is more firmly joined to the tergum but is usually recognizable nevertheless. This condition, however, is distinctly different from that in the Miriformes since it results from a reduction of the ovipositor and the first gonapophyses remain attached to their coxopodite, while in the Miriformes the fusion results from a specialization of the ovipositor in which the gonapophyses become detached from the coxopodites. In other Cimicomorpha which retain their first gonapophyses, such as the reduviids, these appendages are always attached to their coxopodites (although they lose the inner

ramus to the ninth paratergite) and the coxopodites are usually clearly delimited. Thus it appears that the fusion of the first gono-coxopodite to the eighth paratergite and the accompanying loss of the outer ramus from the first gonapophysis is a condition unique to the Miridae and the Tingidae.

An excellent survey of the various kinds of organs assuming the function of the spermatheca in the families of Cimicomorpha has been provided by Carayon (1954). This and previous studies show that the organ serving as the spermatheca in other Heteroptera is absent or does not function as such in the Cimicomorpha. In most Tingidae, Anthocoridae, Microphysidae, Pachynomidae, and Cimicidae the true spermatheca is absent. It has more recently been shown to also be absent in the Thaumastocoridae (Drake and Slater, 1957). Carayon's review indicates that the true spermatheca is usually present in the Miridae, Isometopidae, Joppeicidae, and Reduviidae, but in these families it has lost its original function and in most cases now serves as an accessory gland.

Generally the function of the spermatheca in each family is assumed by two types of organs, one an organ which receives the spermatozoa and the other an organ in which they are stored. In the Reduviidae, Miridae, Tingidae, and most nabids, Carayon points out that the spermatozoa are received by median or paired ectodermal sacs on the anterior genital chamber or on the common oviduct. In the reduviids the spermatozoa are apparently stored in these organs, but in the remainder the spermatozoa apparently migrate to the pedicels of the lateral oviducts where they persist for some time. A distinctly different type of insemination is found in the Cimicidae, Anthocoridae, and some Nabidae, the spermatozoa being injected through a puncture in the body wall usually into a mesodermal receiving organ such as the organ of Berlese of *Cimex lectularius* (Linn.). From here the spermatozoa migrate through the hemocoel, or by way of tissue bridges, to the wall of the lateral oviduct where they are stored in special organs.

Carayon indicates that the manner in which the spermatozoa are stored in the Pachynomidae is unknown and suggests that they are received by a median, anterior sac on the genital chamber similar to that of mirids. However the present authors find that the pachynomids *Aphelonotus simplus* Uhler and *Punctius alutacius* Stål have tubular pseudospermathecae precisely like those of the reduviids. Since these two families are closely related, it seems likely that the pseudospermatheca of pachynomids also serves for sperm storage.

Fig. 51.   Leaf-curl gall formed on *Dichopetalum cymosum* Eng. by *Onymochila dichopetali* (Horváth).

In the Joppeicidae and Microphysidae Carayon finds no special organs for receiving the spermatozoa which are nevertheless stored in the ovarian pedicels. In the tingid Subfamily Vianaidinae the present study shows that sperm receiving organs are absent; the spermatozoa presumably go to the ovarian pedicels but more study of this question is needed.

The fact that the sperm-receiving organs, or seminal sacs, are paired and ectodermal in the Tingidae, as are the comparable organs (pseudospermathecae) of the Reduviidae, is used by Pendergrast (1957) as evidence of a relationship between these two families. Carayon (1954) has emphasized that both histologically and functionally the seminal sacs of tingids are very similar to the median unpaired seminal sac (*cf.* seminal depository, Davis, 1955) of mirids. In most Tingidae the seminal sacs arise from the anterior end of the genital chamber while the pseudospermathecae of Reduviidae arise laterally from the common oviduct. However, in the tingid *Kapiriella maculigera* (Horv.) Carayon (1954) finds that the seminal sacs arise laterally from the common oviduct and are, in this respect, similar to the pseudospermathecae of reduviids. He therefore concludes on the basis of these and other anatomical characters that the natural position of the Tingidae is between the Miridae and Reduviidae.

Since it appears to be rather important in establishing the family relationships of the Tingidae, the question of the homologies of their seminal sacs requires further consideration. First it is necessary to establish the precise location of the seminal sacs. Passing anteriorly from the genital chamber, the genital tract immediately diverges obtusely into lateral oviducts. Therefore the common oviduct is extremely short or non-existent but since the basal portions of the lateral oviducts are ectodermal they are presumably derived from the common oviduct. The seminal sacs generally arise from the anterior mesal surface of the tract in the vicinity of the merger of the lateral oviducts with the genital chamber and frequently it is an arbitrary matter whether we state that they arise from the genital chamber, common oviduct, or from the base of the lateral oviducts since the distinction between these components is itself somewhat arbitrary. In some, such as species of *Tingis*, the seminal sacs rather clearly arise from the mesal surface of the lateral oviducts and in species of *Kapiriella* they arise laterally from the oviducts but these differences in position appear to be of little significance. Furthermore, *Kapiriella* is a rather highly evolved and specialized tingid genus and therefore one may reasonably surmise
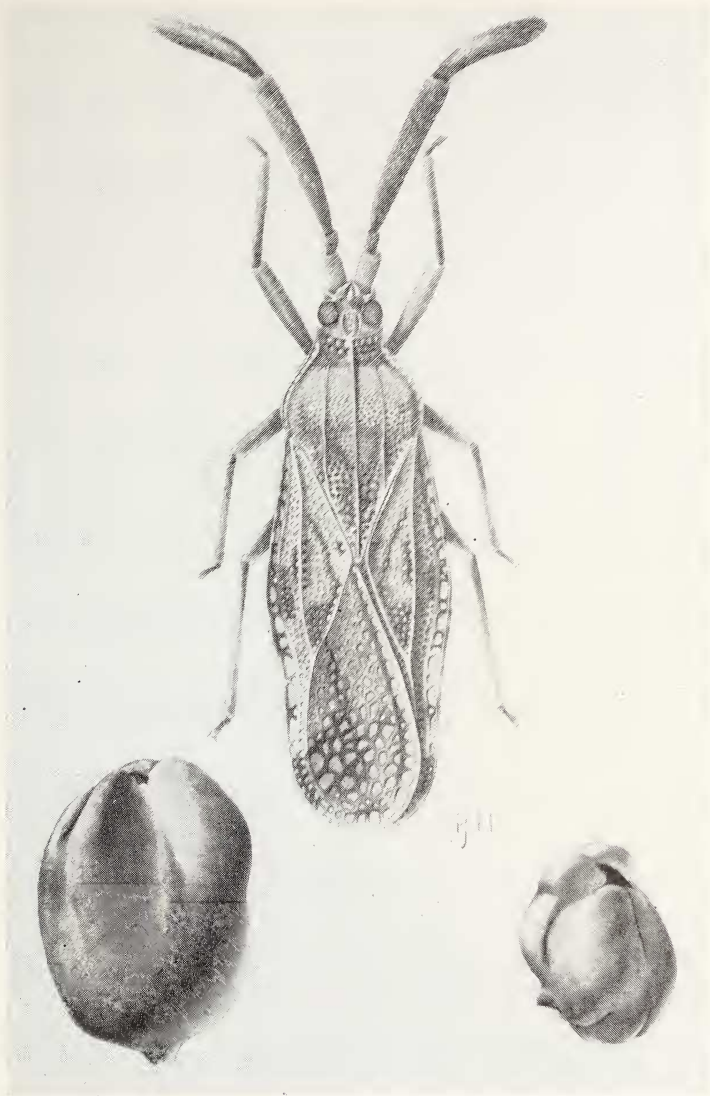
54

Fig. 52.   *Paracopium hamadryas* (Drake) and two floral cecidia formed on *Clerodendron sp.,* Uganda, Africa.

that the position of the seminal sacs in this genus is one secondarily acquired and has no bearing on the question of the relationship of the tingids to the reduviids.

Since the Cantacaderinae, which are in most respects the least specialized of the tingids, lack seminal sacs, it is conceivable that these organs evolved after the family had become a distinct entity. If this were the case then the seminal sacs of tingids would be unique organs, but it is of course also quite possible that the cantacaderines have secondarily lost these structures. In fact the striking histological and functional similarities of these organs to the comparable organ in the Miridae strongly supports, we believe, the contention that the seminal sacs of tingids and mirids have a common origin and thus are homologous. It is problematical whether in the primitive condition the seminal sacs were paired or median but it is noteworthy that the areas of glandular epithelium of the seminal sac of mirids is paired. Furthermore, we feel that in most respects the female genitalia of tingids are less specialized than those of the mirids. That the pseudospermathecae of reduviids is homologous to the seminal sacs of tingids and mirids remains a distinct possibility but if these organs do have a common origin, the pseudospermathecae have diverged from the seminal sacs to such an extent as to make this question very difficult to resolve at present.

In the Reduviidae the eighth segment is reduced to a ventral sclerite and the ninth segment (pygophore) is deeply telescoped into the seventh so that at rest all but its posterior ventral surface is covered. In the tingids and other cimicomorph families the eighth segment is not reduced and the pygophore is exposed dorsally.

The parameres are symmetrical in the reduvioids, Tingidae, Joppeicidae, Nabidae, and Microphysidae. They are very asymmetrical in the Anthocoridae, Thaumastocoridae, Cimicidae, and Miridae; in all of these families but the Miridae one paramere, usually the right, is vestigial or absent. The development of asymmetry probably represents a specialization for a mating position in which the male is always on the same side, usually the right, of the female.[3] This specialization appears to have arisen independently

---

[3] Drake and Slater (1957) reported that in the thaumastocorid, *Xylastocoris luteolus* Barber, both dextral and sinistral males are found. According to Baranowski (1958) the normal habitat of the female is a crevice and so she may be approached by the male from one side only. Thus sinistral males may mate with females with their right side exposed and *vice versa*.
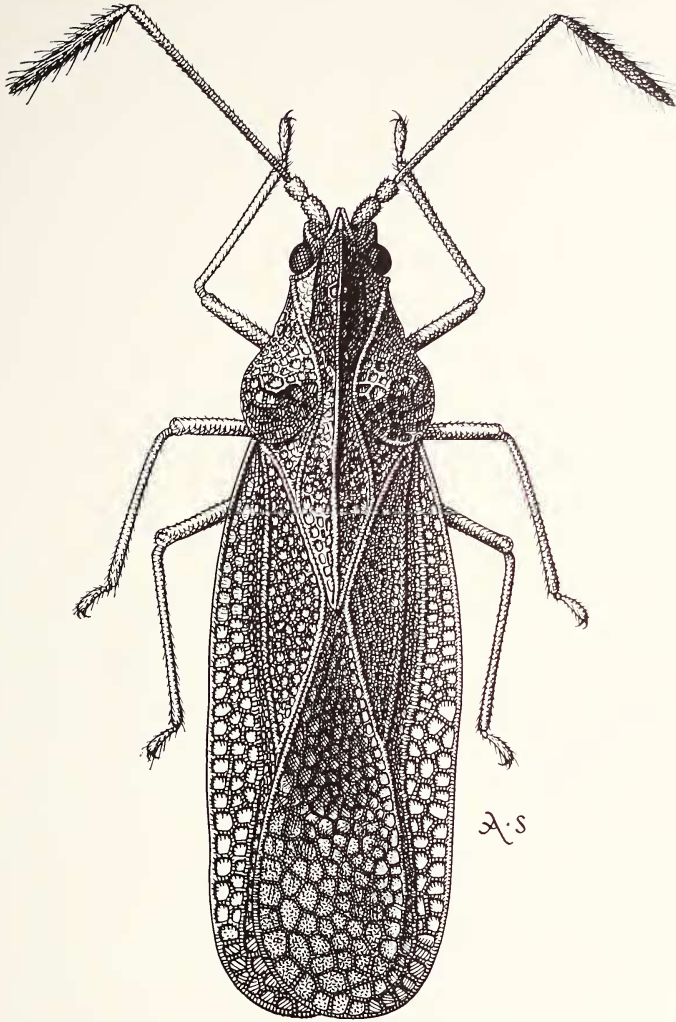
Fig. 53.   *Baeochila nexa* (Distant).

several times in the Cimicomorpha. The parameres of reduviids are very predominately symmetrical but some asymmetry has evolved in the piratines. The mirids have predominately asymmetrical parameres but those of the Isometopinae are symmetrical. The parameres of the Microphysidae are symmetrical while those of their close relatives, the Anthocoridae, are asymmetrical. Thus the asymmetry of the parameres does not appear to be of much phylogenetic significance at the family level.

There appear to be two types of positions assumed by the parameres (at rest) in the Cimicomorpha. In most Reduviidae, Tingidae, and Miridae the parameres lie folded across the end of the pygophore while in most Nabidae, Pachynomidae, Anthocoridae, Cimicidae, Thaumastocoridae, and Joppeicidae the parameres are folded over the top of the pygophore or along its side. Further study is necessary, however, to evaluate the phylogenetic significance of these two types.

The descriptions of the parameres of the Microphysidae (China and Meyers, 1929, and China, 1953) indicate that these appendages arise from along side of the basal plate and lie on each side of the phallus in the genital chamber and thus do not fit into either of the types described above. The close association of the parameres with the basal plate appears to be an unusually primitive condition. Phylogenetically and ontogenetically, the parameres of insects are believed to originate as lateral subdivisions of the phallus. They remain proximal to the phallus in the auchenorrhynchous Homoptera but in the Heteroptera they generally have evolved a secondary association with the margin of the genital capsule and have become separated from the phallus.

Certain features of the phallus are very important as distinguishing characteristics of the Cimicomorpha and also are often important at the family level or lower but no superfamily characteristics of the phallus have yet been developed. Singh Pruthi (1925) has noted certain similarities of the tingid phallus to that of Reduviidae as well as to the Miridae and Nabidae but the similarities he mentions involve either characteristics which now apply to the Cimicomorpha in general or else involve vague similarities in general appearances and shape.

The reduviid phallus may be characterized by its mid-ventral extension of the basal plate, by internal supporting sclerites termed struts, and by the subdivision of the phallosoma into a basal and distal section. In the closely related Pachynomidae the basal plate is like that of the reduviids but struts are lacking. In the Thaumastocoridae the basal plate also has a mid-ventral extension and
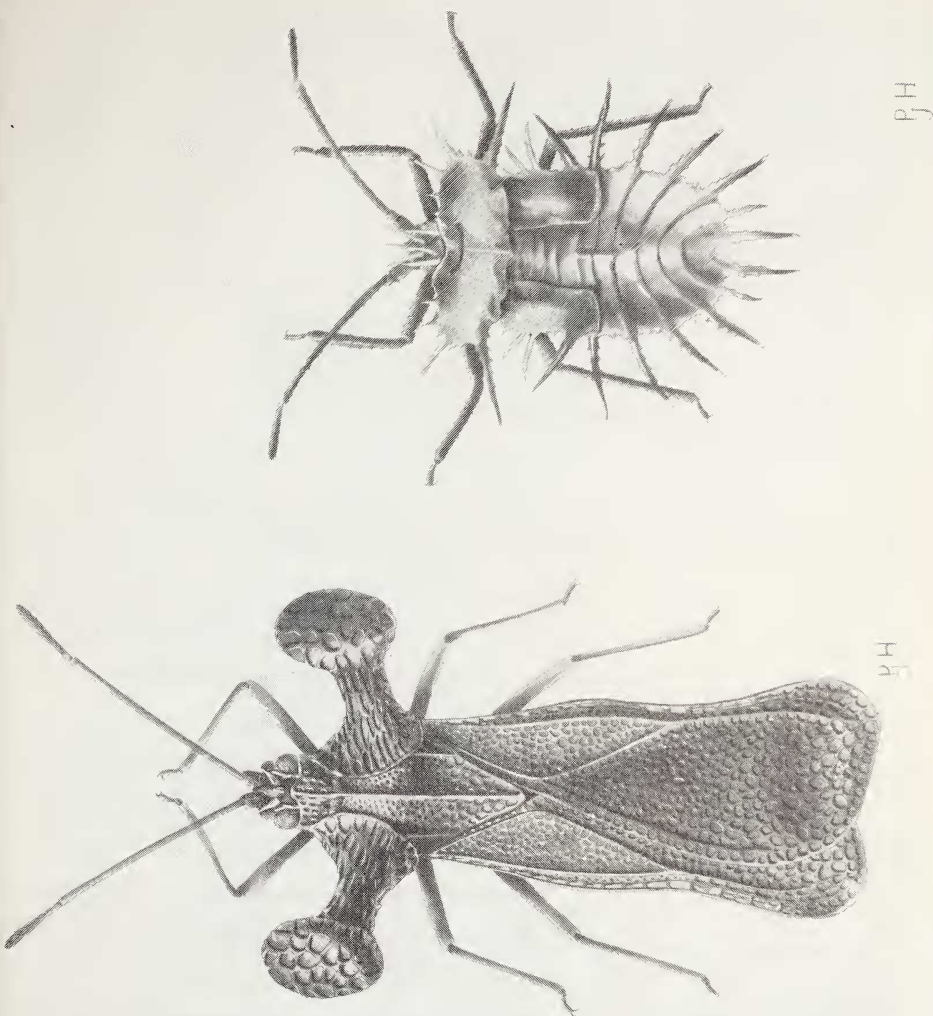
Fig. 54.   *Diconocoris capsui* Horváth.
Adult and Nymph

the phallosoma is subdivided. The most distinctive feature of the nabid phallus is the ejaculatory duct, which is reinforced by sclerotized rings. The phallus of the mirids may be of quite diverse form and is thus difficult to characterize, but in most cases it is asymmetrical and has complex processes arising from the endosoma. The phallus of anthocorids and cimicids is reduced and specialized for extending along the groove in the paramere. This specialization is associated with the unique types of intromission and insemination found in these families. The phallus of Joppeicidae (China, 1955) and Microphysidae (Chain and Myers, 1929; China, 1953) is distinctively long and slender and not differentiated into phallosoma and endosoma. Since the arrangement of the parameres in Microphysidae appears to be a primitive condition similar to that of the auchenorrhynchous Homoptera, the undifferentiated phallus of microphysids may be primitive and similar to the phallus of many Auchenorrhyncha.

The tingid phallus, aside from a general resemblance in shape to the nabid phallus, does not share any unique features with any of the above mentioned families except perhaps the Miridae. In these two families the apex of the phallosoma in repose extends from the orifice of the genital atrium, forming an operculum for this orifice. In the reduviids the phallus in repose is completely within the genital atrium and the orifice is covered by flaps folding over it from each side. As far as we know, the characteristic resting position of the phallus in tingids and mirids is not found in other cimicomorphs.

Both ectadene (ectodermal) and mesadene (mesodermal) accessory glands may be associated with the male reproductive tract in the Heteroptera, and since the form of these glands is more or less distinctive for each family, they are therefore of possible use in showing family relationships (Carayon, 1950; Pendergrast, 1957). Unfortunately, the structure of these glands is unknown at present in several minor groups of the Cimicomorpha (such as the Microphysidae, Velocipedidae, Thamastocoridae, and Joppeicidae) and a study of them should provide valuable evidence bearing on the phylogeny of these groups. The cimicids and anthocorids lack ectadenia and the mesadenia consist of thin, branching tubules which enter a sac-like reservoir which in turn leads to the ejaculatory bulb. In the Nabidae ectadenia are present and the mesadenia are essentially the same as those of the cimicids and anthocorids. Carayon (1950) has noted this similarity as evidence that the nabids are more closely related to these latter families than to the reduviids which have
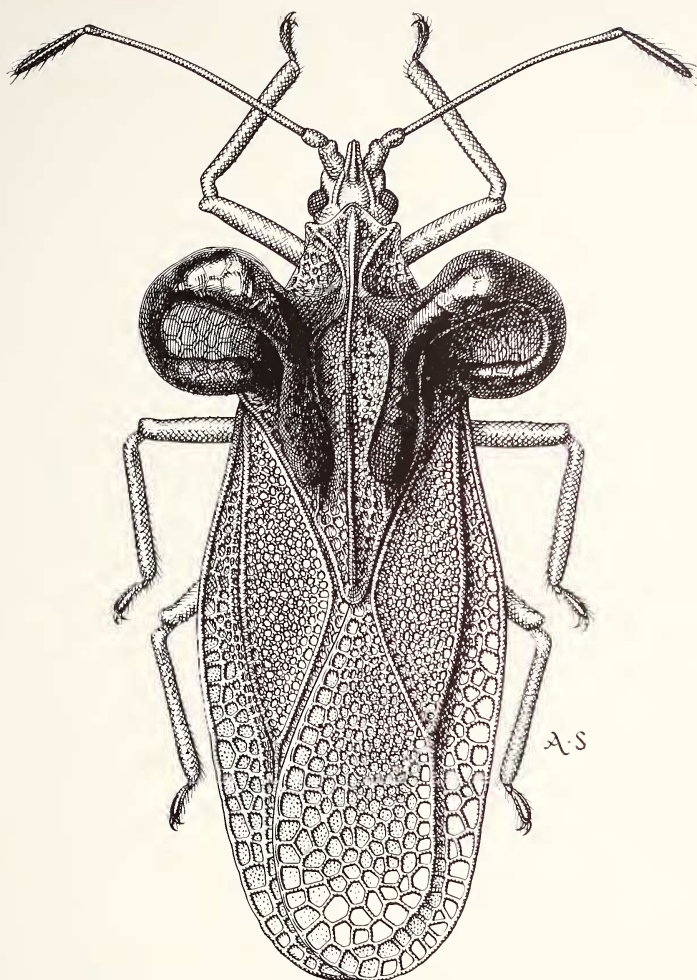
Fig. 55.   *Elasmognathus helferi* Fieber.

mesadenia consisting of three to five thick lobes converging on a thin duct which leads to the ejaculatory bulb. On each side of the ejaculatory bulb the reduviids often have a small structure termed the ampulla (Galliard, 1935) and these may represent ectadenia.

The male accessory glands of mirids have been described by Kullenberg (1947). In this group the ectadenia are apparently lacking and the development of the mesadenia is quite elaborate. A pair of relatively large, long tubular glands extend laterally from each side of the ejaculatory bulb and smaller, variously developed glands
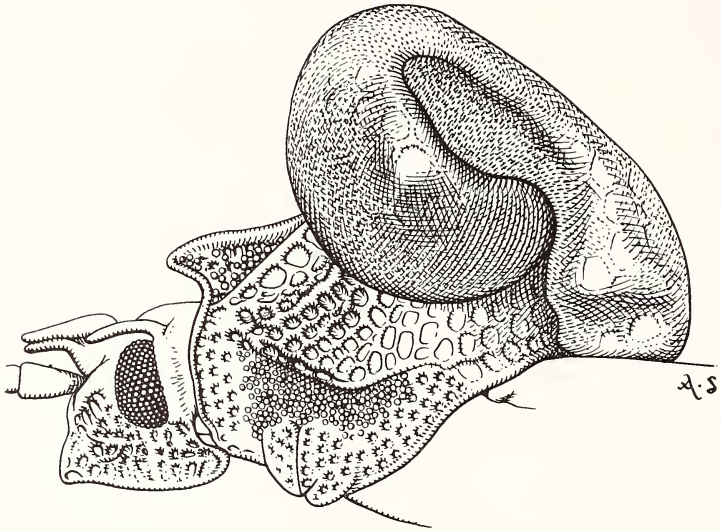

Fig. 56. *Elasmognathus helferi* Fieber, profile of head and pronotum.

extend from the mid-ventral and mid-dorsal surface of the bulb. Carayon (1958) indicates that the accessory glands of the isometopids are essentially the same as those of the mirids.

The accessory glands of the tingids, as represented by the Tinginae, are not strikingly similar to the glands of any of the families described above but perhaps have certain features in common with the mirids. The principal glands of tingids are simple long tubes extending from the ejaculatory bulb like those of the mirids. Although Pendergrast (1957) has reported that the tingids have ectadenia, the present study shows that these glands lack a cuticular intima and are therefore probably mesadenia; they are possibly

homologous to the outer lateral mesadenia of the mirids. On the other hand the tingids apparently lack the dorsal and ventral accessory gland found in the mirids. It is fortunate that the accessory glands of the cantacaderine tingids are poorly known since this group is in many respects the most generalized of the tingids and may therefore have glands which give clearer phylogenetic evidence.

The ejaculatory bulb of tingids is similar to that of mirids and unlike the organ in other cimicomorphs in so far as is known. As
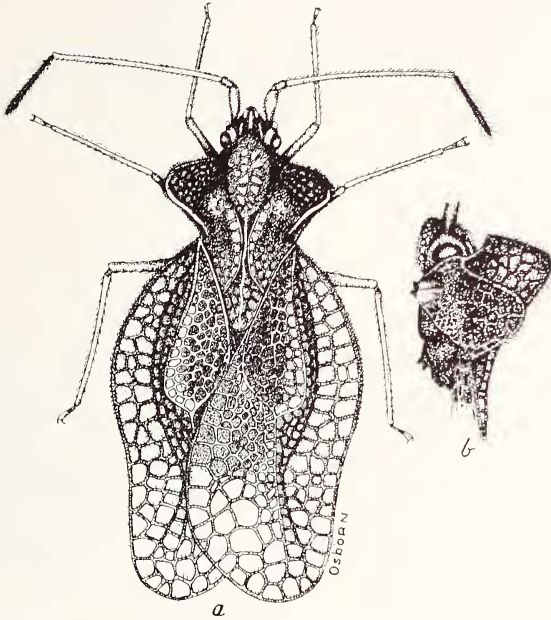
Fig. 57. *Pachycysta championi* Drake, **a**, dorsal and **b**, lateral aspects.

Carayon (1958) has pointed out, the ejaculatory bulb of mirids, in contrast to that of the cimicids and anthocorids, has a relatively large lumen and thin walls with reduced muscularis and cuticular intima. The ejaculatory bulb of tingids also has these features and in both the Miridae and Tingidae the bulb is joined to a very short ejaculatory duct and is contiguous with the basal plate. In other cimicomorphs the ejaculatory duct typically extends distinctly out from the basal plate before entering the ejaculatory bulb.
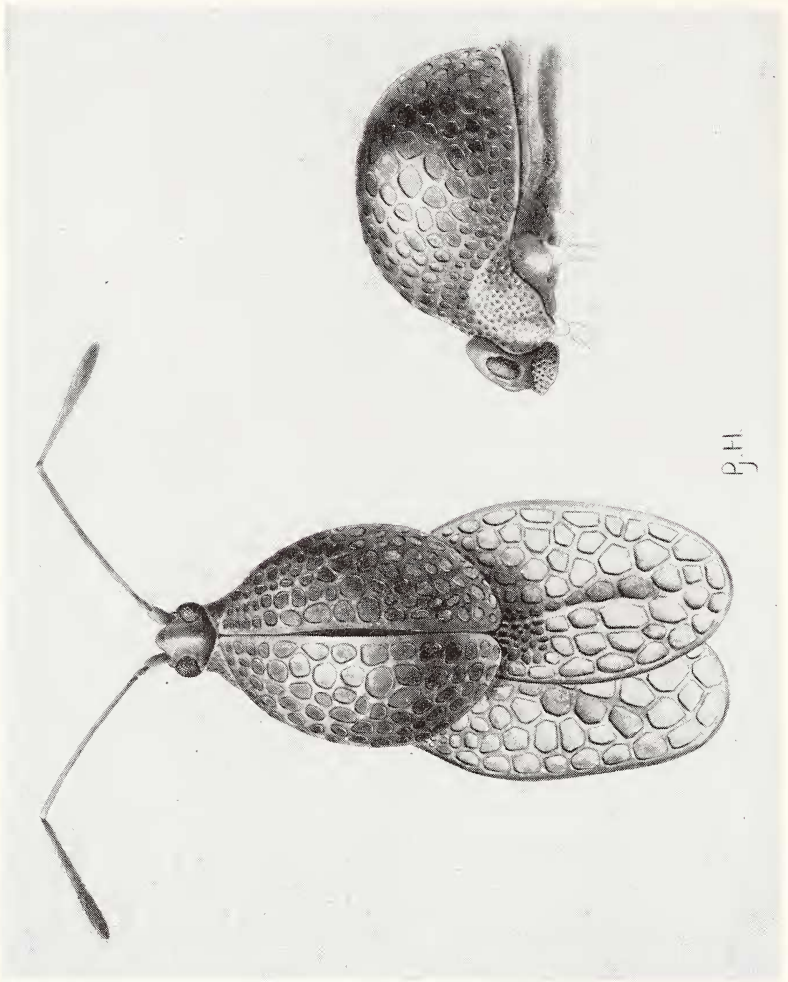
Fig. 58.   *Holophygdon melanesica* Kirkaldy.

Phylogenetic Position of the Tingidae

That the tingids are most closely related to the Reduviidae has been suggested because they apparently have in common three rather distinctive features, paired metathoracic scent gland reservoirs, paired ectodermal sperm storage organs arising from the oviduct, and rotatory metacoxae. It has been noted in the preceding section that the rotatory type metacoxa and the paired condition of the scent gland reservoir have evolved independently in at least
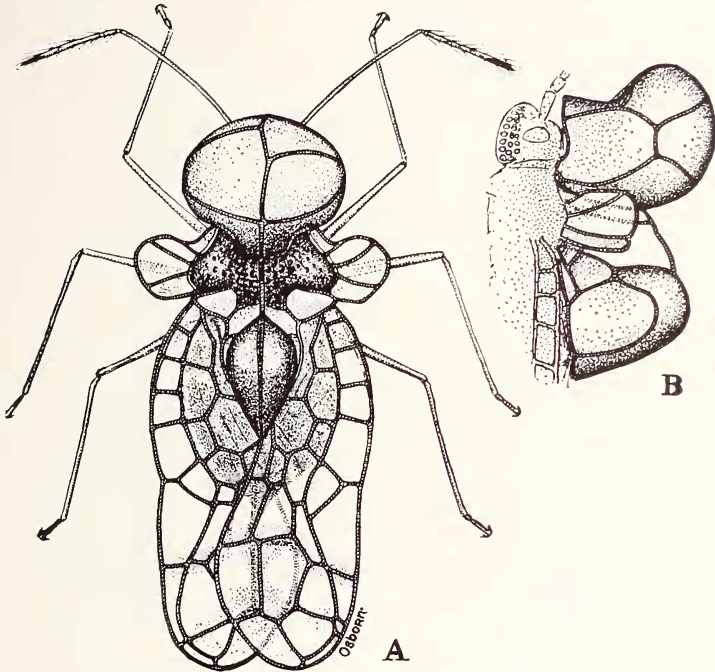

Fig. 59. Aepycysta schwartzi Drake.

some heteropterons, and there is a strong possibility that these features originated independently in the Tingidae and Reduviidae. Furthermore the scent glands and the sperm storage organs in these two families, although similar in being paired, differ in details of their anatomy, histology, and perhaps their function. In view of the doubtful phylogenetic significance of these similiarities as well as the otherwise great dissimilarities, both anatomical and biological, of the Tingidae and Reduviidae, we must conclude that these two families are not very closely related.

The Tingidae are similar to both the Miridae and the cimicoid families with regard to their lack of the first abdominal spiracles and ventral connexival sutures, and the pattern of the hind wing venation. In addition they resemble the Miridae and differ from the cimicoid families in several significant features cited in the preceding section. Of particular interest is the similarity of the Tingidae and Miridae in their head shape, in usually lacking ocelli, in
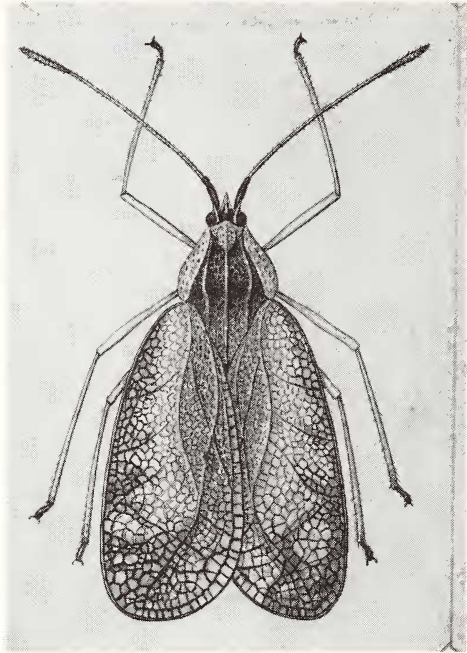

Fig. 60. *Leptodictya ochropa* (Stål).

having a fully four-segmented beak, in their having an ovipositor with the first gonapophysis detached from its gonocoxopodite and the latter fused to the eighth paratergite, and in characteristics of their seminal sacs, mesadenia, and ejaculatory bulb. Furthermore, the Tingidae and Miridae are very similar in their general biology, both being primarily phytophagous (tingids entirely and mirids largely phytophagous) and often having restricted host plant relationships. The other cimicomorphs, in contrast, are predominately predacious or parasitic with the exception of Thaumastocoridae.
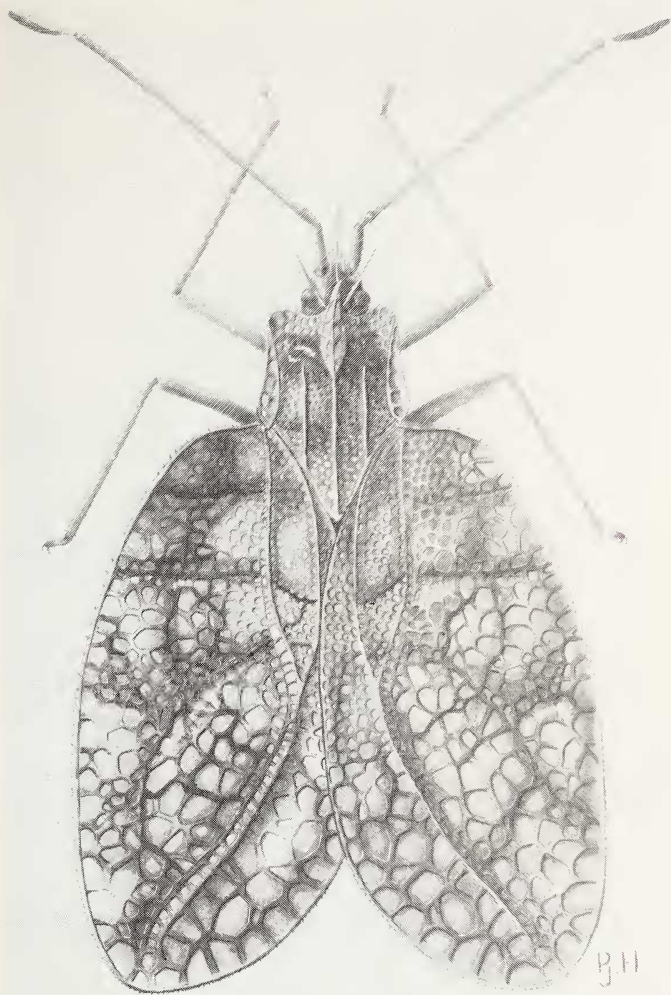
Fig. 61.   *Leptodictya* (*Hanuala*) *leinahoni* Kirkaldy.

It seems likely that the Heteroptera diverged from an ancestoral phytophagous hemipteran stock through the acquisition of the predatory habit and the attendant modifications of the beak and development of the gula. Consequently it is probable that the cimicomorphs were primitively predacious and the parasitic and phytophagous habits were developed secondarily. Whether the phytophagous habit evolved independently or had a common origin in the Tingidae and Miridae is a matter of considerable importance in evaluating the significance of the features that these groups have in common. If their food habits were of independent origins then their similarities in head structure and beak, all being related to some extent to plant feeding, could very well be convergent characteristics. However, the characteristics that they share with regard to their ovipositor, seminal sacs, mesadenia, and ejaculatory bulb are not related to their food habits and therefore lack any common selective factor which might have brought about their convergent evolution and must be similar as a result of a common origin. This being so, it then seems likely that the similarities in food habits and in the other morphological features of tingids and mirids must also be a result of a common ancestry.

Of the two groups the mirids are by far the more primitive in structure. This generalization refers not only to their lack of the elaborate, lacy ornateness of the pronotum and hemelytra so characteristic of the tingids but to the more primitive structure of the thorax, metathoracic scent glands, abdominal segmentation, and tarsal segmentation as well. On the other hand, the bilaterally symmetrical male genitalia of the tingids represents a condition more primitive than that found in the mirids.

From the foregoing considerations, we conceive of the ancestral line of the mirids and tingids as diverging early from the cimicomorph stock as a phytophagous group. The mirids have retained in most respects a relatively primitive structure while the tingids have become highly modified and superficially, at least, bear little resemblance to the mirids. Next to the tingids, the mirids appear to be most nearly related to the Anthocoridae. However as has been recently pointed out by Carayon (1958), the Miridae and Anthocoridae have a number of phylogenetic characteristics such as those of their beak, ovipositor, mesadenia, ejaculatory bulb, spermathecal organs, and mode of fecundation which distinctly set them apart. We therefore choose to remove the Miridae from the superfamily Cimicoidea (Reuter, 1910) and place them in a superfamily Miroidea, redefined from that established by Kirkaldy (1906).
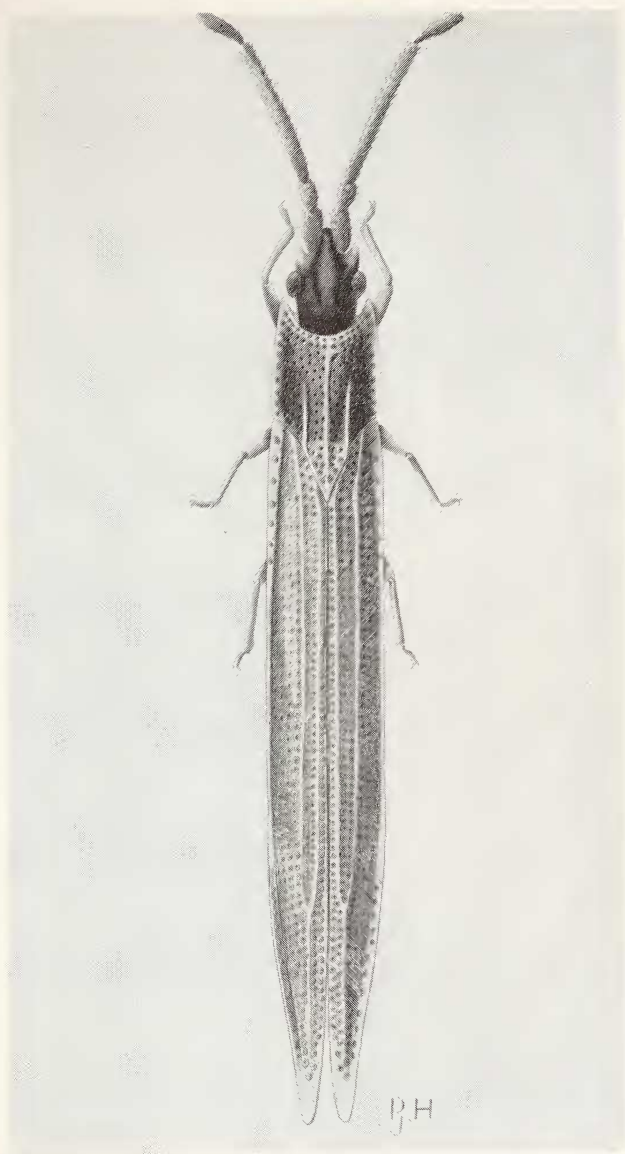
Fig. 62. *Perbrinckea brincki* Drake.

SUPERFAMILY MIROIDEA, *sensu novum*

The Superfamily Miroidea, as herein constituted, comprises the families Tingidae and Miridae. In this new conception, the Miroidea may be defined as follows: Primarily phytophagous; head usually declivent, ocelli usually absent (except Isometopinae), beak fully four-segmented; arolia usually present; thoracic scent gland
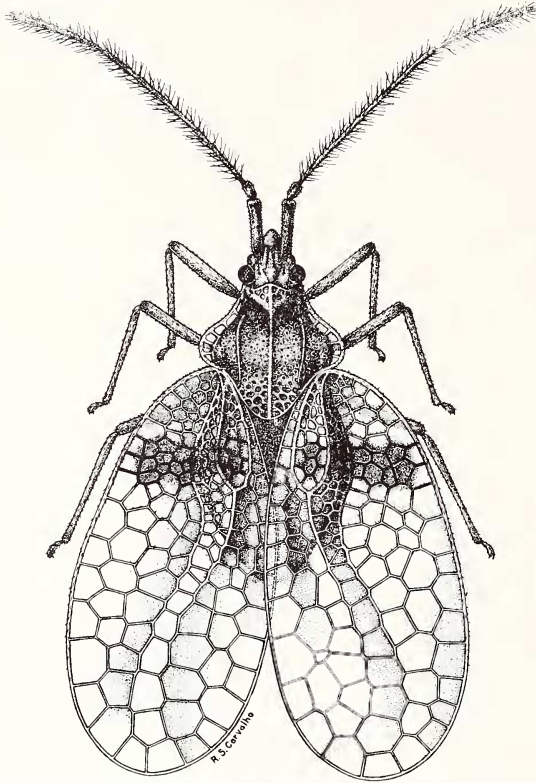

Fig. 63. *Pliobyrsa mollonediae* (Drake and Hambleton).

ostioles usually present; hind wing venation lacking a hamus, **Pc** and **1st A** basally fused and distally divergent; first abdominal spiracles absent; ovipositor well developed, enclosed at rest by second gonocoxopodites, first gonapophysis free of its gonocoxopodite, first gonocoxopodite fused to eighth paratergite; parameres convergent at rest.

The characters separating Tingidae from Miridae are as follows: Forewings of uniform texture throughout, without membrane,

fracture, and cuneus, the embolium absent; clavus well developed and usually demarcated in Cantacaderinae, narrow and concealed beneath hind pronotal process in Tinginae, indistinguishable from corium in Vianaidinae; scutellum small, either visible or hidden beneath hind margin or pronotum in Cantacaderinae; always covered with posterior pronotal projection in Tinginae, a little larger and fully exposed in Vianaidinae; metathoracic scent glands paired (fig. 7), ostiole and ostiolar sulcus almost always present on each metapleuron (figs. 4, 5, 6, 48, 75), tarsi two-segmented, claws paired, without arolia or pseudoarolia, each claw usually with a small tusk near the base of inner margin; antennal segmentation as described in key to subfamilies and illustrations (figs. 3, 5, 6, 46, 66). Other significant features are the singular and assorted lace-like outgrowths of the collum, carinae, paranota, and posterior process of the pronotum and of the elytra in the Subfamilies Tinginae (figs. 43, 44, 49, 71), and Cantacaderinae (figs. 28, 29, 30). The degenerate compound eyes (without or with only a small number of facets) and the prominent T-shaped, ostiolar channel with large, roughened, evaporating area (figs. 72, 74, 75) are also distinguishing features in the vianaidines.

Systematics of the Family Tingidae

Type genus, *Tingis* Fabricius.

The family Tingidae, as systematized here, comprises 1,784 species, separated into 220 genera, including both living and zoolithic forms. A breakdown into subfamilial groups gives these taxonomic figures: Tinginae with 1,692 species in 197 genera; Cantacaderinae with 89 species in 21 genera; Vianaidinae with 3 species in 2 genera. In distribution, tingines are world-wide, the cantacaderines inhabit all faunal regions except the Nearctic (America north of Mexico), and the myrmecophilous vianaidines are found in the Neotropical Region—Trinidad (British West Indies), Bolivia, and Argentina.

The fossil records are too scant to tell much about the phylogeny and chorology of tingids during geologic times of many million-years gone by. According to Drake and Ruhoff (in press), 3 species and 2 genera (*Cantacader* and *Phatnoma*) of cantacaderines are recorded from molds in Baltic and Prussian ambers, and 11 species and 4 genera of tingines (*Dictyla, Celantia, Eotingis,* and *Tingis*) from petrified forms in stone. The vianaidines are unrecorded as fossils. The fossil records do not include extinct species cited in the literature only as "*Tingis* sp." The genus *Eotingis* is not rep-

resented by living species. The fossil species, placed in *Cantacader,* *Phatnoma,* and *Dictyla,* are largely typical members of these genera, and they differ only specifically from existing species in these respective genera.

As stated previously, the subfamily classification of the Tingidae had its inception in Stål's divisions of the subfamily Tinginae. With the raising of Tinginae to the familial rank, these divisions later became established as subfamilies Cantacaderinae, Tinginae, and Agrammatinae (= Serenthiinae).

Based upon anatomical characteristics as established in the preceding pages, the Subfamily Agrammatinae has been synonymized with the Subfamily Tinginae and the Family Vianaididae reduced to the subfamilial level. These nomenclatural changes are discussed further in the forthcoming pages under their respective subfamily captions.

The subfamily key, as formulated below, embodies all taxonomic changes being made here in the subfamily classification of the Tingidae.

Key to Subfamilies of Tingidae

1. Dorsal surface finely to coarsely punctate, not lacelike in appearance; compound eyes vestigial, without or with only a few facets; antennae with first segment usually shortest, second and third segments subequal in length or the latter slightly longer, fourth segment longest; pronotum noncarinate; scutellum triangular, plainly visible; metathoracic scent glands with ostiole and ostiolar canal on each metapleuron very pronounced, the sulcus raised, ypsiliform, with evaporating area very large, roughened, overspreading metapleuron, hind part of mesopleuron and downward onto the sternum; abdominal sterna two through five fused, other segments free; brachypterous; macropterous forms unknown (figs. 72, 73, 74, 75).

Subfamily **Vianaidinae** Kormilev

Dorsal surface finely to coarsely lacy, veinlets forming boundaries of areolae slightly raised; compound eyes normal, fully developed, with many facets; antennae with second segment usually shortest, sometimes first and second segments both short and subequal to each other in length; third segment almost invariably longest (third and fourth segments rarely both long, slender, and subequal in length
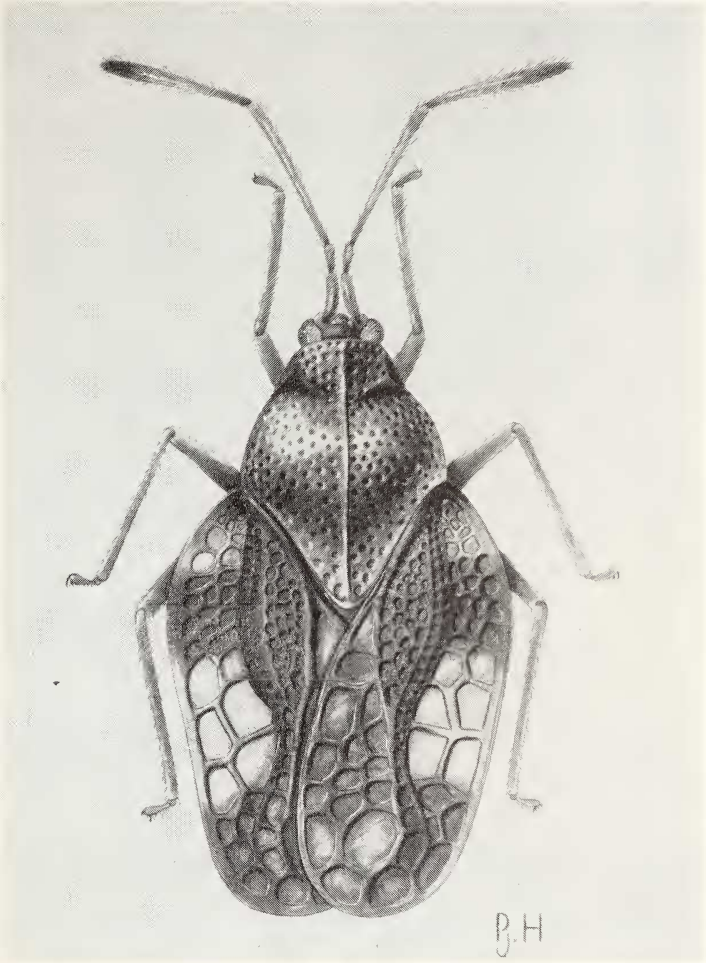
Fig. 64. *Orotingis muiri* Drake.

as in Genus *Macopharsa* fig. 48), fourth segment short to moderately long, fusiform to clavate in form; metathoracic scent gland with ostiole and ostiolar sulcus (rarely vestigial) on each metapleuron, with channel nearly upright (fig. 4); abdominal sterna two and three or two through four fused, other segments free; pterygopolymorphism known in many species (figs. 28, 37, 57, 65, 70) 2

2. Head long, longly produced in front of compound eyes, moderately porrect, without armature or armed with one to nine tubercles or spines; bucculae long, wide, usually projected forward beyond apex of clypeus; antennae with second segment not surpassing apex of head; pronotum uni-, tri-, or quinquecarinate (figs. 29, 30, 31), the hind margin at most only slightly but very widely produced backwards, never triangularly prolonged posteriorly so as to spread over the clavus, with the margin very wide, sinuately or obtusely truncated; scutellum small, either visible (fig. 32) or concealed (fig. 28) under margin of pronotum; clavus (fig. 30) well developed, rarely fused with discoidal area, then only feebly demarcated (fig. 28); abdominal sterna two and three fused, other segments free (figs. 28–31).

Subfamily **Cantacaderinae** Stål

Head generally short, strongly declivent, very little produced in front of eyes (extended anteriorly and much less declivent in such genera as *Biskira*, *Dictyonota* (fig. 35). *Ypsotingis* (fig. 36), and *Dictyonotingis* (fig. 37); bucculae long, terminating anteriorly along lateral sides of labium, or more often, longer with anterior ends curved inward and frequently meeting mesad in front of base of labium so as to close anteriorly the buccal sulcus (fig. 4); second antennal segment greatly surpassing apex of head (except in such genera as *Ypsotingis* (fig. 36), *Dictyonota* (fig. 35) and other tingine genera with very long heads); pronotum uni- or tricarinate (figs. 34, 49), hind pronotal margin always triangularly prolonged backwards (figs. 32, 34, 44, 64) so as to overspread and conceal scutellum and clavus of both elytra in repose; abdominal sterna two through four fused, other segments free (figs. 1, 42, 45, 60, 70).

Subfamily **Tinginae** Laporte

SUBFAMILY CANTACADERINAE STÅL

This family comprises a comparatively small, sharply defined group. Its members occur rather sparsely in all major land areas of the world, except the Americas north of Mexico. In a number of respects, the cantacaderines are the most generalized and most primitive of the tingid subfamilies.
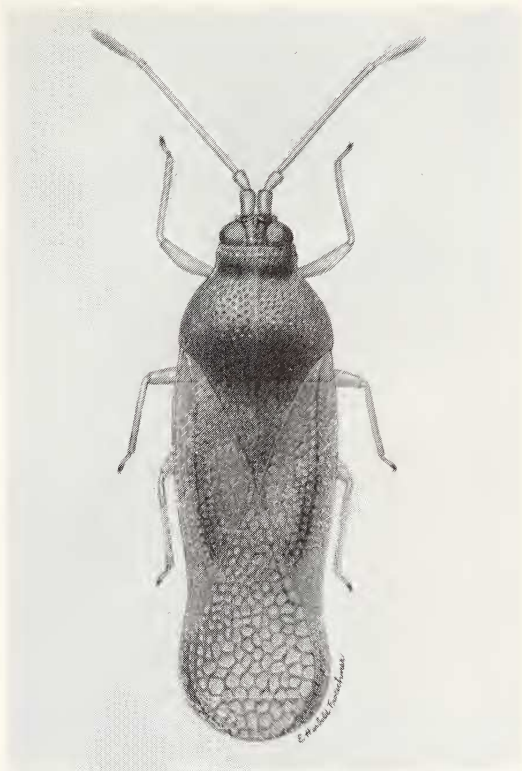

Fig. 65.   *Perissonemia sodalis* Drake.

The salient characters separating the Cantacaderinae from the other tingids are included in the comprehensive key to the subfamilies.   The type genus and its type species, *Cantacader quadricornis* (fig. 28) was used in the morphological studies.   The adult of that species and four other cantacaderines have been illustrated (figs. 28–31).

Besides the characters customarily employed in taxonomic keys, we have found several other structures of prime importance.

Among these are the following: Fused second and third abdominal sternites; paired metathoracic scent glands; male (figs. 11, 19) and female (fig. 15) genital organs; and the wing venation of mesothoracic (fig. 13) and metathoracic wings (fig. 14).

The forewing was found to be of unusual and significant import. After considerable study, it was observed that the forewings
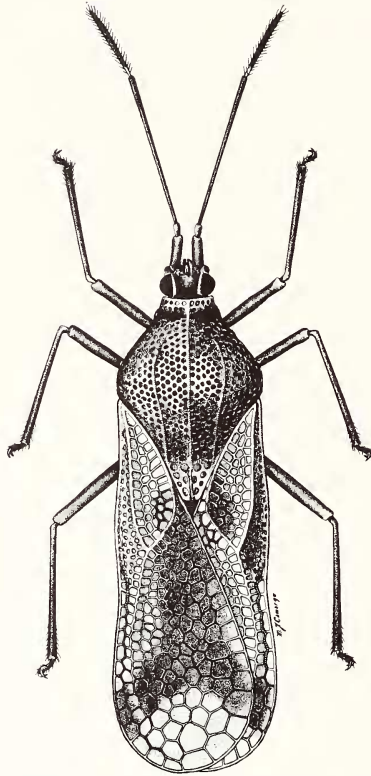

Fig. 66. *Amblystira solida* Drake.

of members of the Genera *Cantacader* (fig. 28), *Allocader, Cerato-cader* (fig. 30) *Nectocader,* and *Teratocader* have the ''costal area'' divided into two quite distinct areas by a prominent, longitudinal vein running parallel to and only one row of areolae removed from the outer marginal vein (figs. 12, 28, 31). As indicated above, this vein is probably the Sc and its position modifies the present conception of the areas and venation of the mesothoracic wing in certain cantacaderines. The Sc vein is not found in this position in the

other genera of Cantacaderinae, nor in the other tingid subfamilies.

Since the **Sc** separates the costal area in the forewing into two parts, we are naming the narrow, uniseriate space between this vein and the outer marginal vein the ''stenocostal area,'' and the space between the subcostal and stenocostal areas remains as heretofore the costal area. On the basis of the stenocostal area and the prominent boundary vein that clearly sets apart the costal and steno-
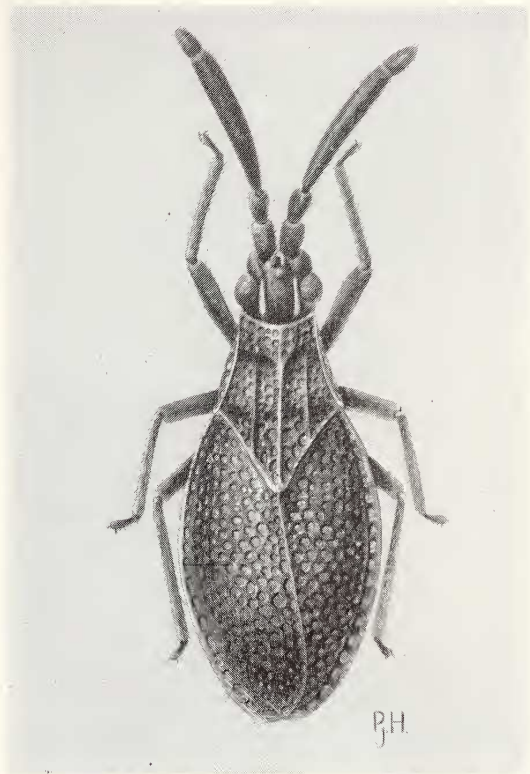

Fig. 67. *Alveotingis grossocerata* Osborn and Drake.

costal areas, we are separating the Subfamily Cantacaderinae into tribes as follows:

Tribe **Cantacaderini** Stål: This tribe is distinguished by the presence of the clearly defined stenocostal area of the elytron. It comprises the Genera *Cantacader* Amyot and Serville (fig. 28), *Allocader* Drake, *Nectocader* Drake, *Teratocader* Drake and *Ceratocader* Drake (fig. 30).

77

Tribe **Phatnomini, new tribe:** This tribe is distinguished by the absence of the stenocostal area. It composes the Genera *Phatnoma* Fieber, *Eocader* Drake, *Malala* Distant, *Cyperobia* Bergroth (fig. 31), *Angiocader* Drake, *Astolphos* Distant, *Pseudophatnoma* Bloete, *Stenocader* Drake and Hambleton, *Recardus* Distant, *Gonycentrum* Bergroth, *Oranoma* Drake (fig. 29). *Cnemiandrus* Distant, *Cyclotynaspis* Montandon, *Ulmus* Distant, *Plesionoma* Drake, and *Zetekella* Drake.
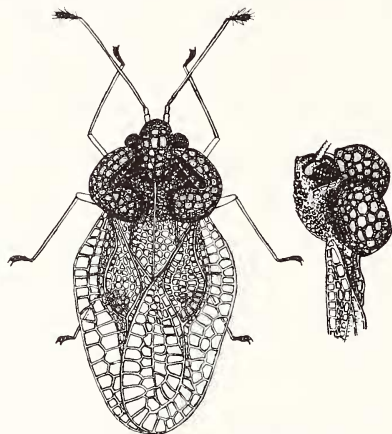

Fig. 68. *Calotingis knighti* Drake

SUBFAMILY TINGINAE LAPORTE

The tingines by far are the largest, most unusually modified, and the most widely distributed of the tingid subfamilies, being well represented in all continents and on most islands. Although slightly better represented palaeontologically, they are structurally less primitive than the cantacaderines.

Since their erection in 1872, the agrammatines and tingines have customarily been classified as separate subfamilies. In contrast to the anatomical characteristics of the Cantacaderinae, the present studies clearly emphasize the lack of consistent and valid taxonomic differences for the separation of these subfamilies from each other.

Customarily the agrammatines have been separated from the tingines on the basis of the following characters: Legs short, with fore femora abruptly swollen near the base and then becoming slender towards or at the apex; pronotum unicarinate, collum without hood, paranota wanting; and the forewing with a narrow costal area, but with the corium not subdivided into areas.

The agrammatine character of short legs and moderately swollen femora is only relative and not of enough significance to be used as a criterion for subfamily differentiation since some tingines, such as *Perbrinckea brincki* (fig. 62), have short legs and moderately swollen femora. Among the tingines with pronotal characteristics like the agrammatines, we might mention such species as *Orotingis muiri* (fig. 64), *Perissonemia sodalis* (fig. 65), *Litadea delicatula* (fig. 39), and *Amblystira morrisoni*. In brachypterous forms of
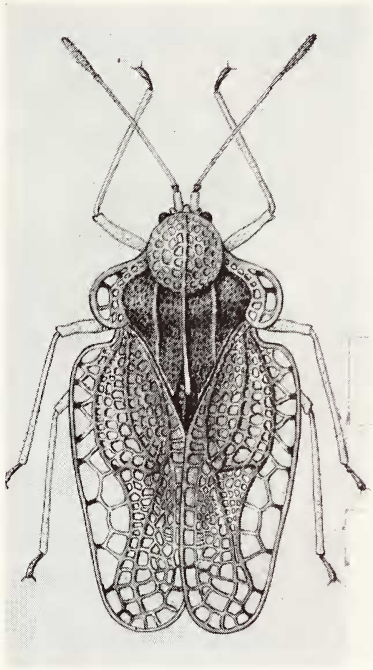
Fig. 69. *Sphaerocysta inflata* Stål

the Genus *Alveotingis* (fig. 67), the elytra are strongly convex, the costal area narrow and uniseriate, and the corium is undivided into areas as in the agrammatines. In fact the corial areas of tingines are not always clearly differentiated even in the macropterous condition.

An examination of numerous species in the Genus *Agramma* Stephen (type genus of Agrammatinae) shows that the presence or absence of divisional areas in the corium is not constant and, to a

limited extent at least, is linked with pterygopolymorphism in some species of this genus as well as in the Genus *Alveotingis* (fig. 67). Brachypterous members of *Agramma* have strongly convex elytra with corium usually undivided but in the macropterous forms of such species as *Agramma lineatum* (Horvath), *A. perinqueyi* (Distant), *A. hapahanum* (Drake & Maa), *A. kivuanum* (Drake, and *A. vulturnum* (Kirkaldy), and other species, we have found that the subcostal, discoidal, and sutural areas of the corium vary from slightly to clearly differentiated.
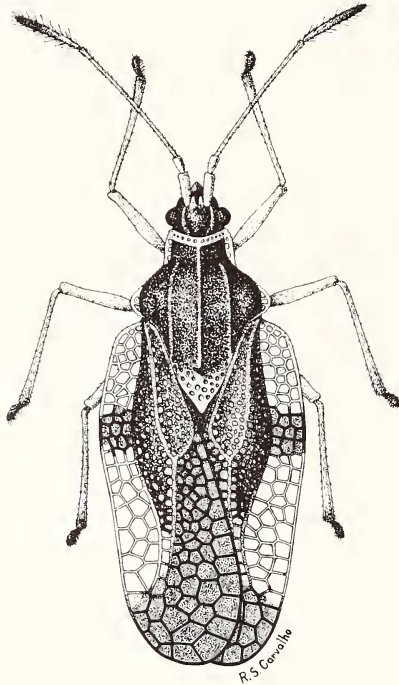
Fig. 70. *Acysta praeclara* Drake and Hambleton.

Since, after thorough study, we have been unable to find any new characteristics for distinguishing the Agrammatinae and since the characters customarily used for their separation are unusable, we therefore are suppressing the Subfamily Agrammatinae as a synonym of the Subfamily Tinginae (new synonym).

In the development of unusual assortments of hyperthrophied projections of the laminar, lacy expansions of the prontal structures and of reticulations of elytra, the tingines by far surpass the

cantacaderines. The myriads of these lacy formations provide the principal structural characters used in generic and specific taxonomy. Many species are adorned with spines on the head (figs. 33, 41, 42, 49), outer margins of paranota and elytra (34, 71), and other parts of the dorsal surface. In a few genera such as *Urentius* (fig. 32), the species are truly myriacanthus in appearance. Members of the genera *Lasiacanthus* and *Inoma* Hacker are also spinosely arrayed. Nymphs (figs. 40, 54) of many genera are armed or unarmed, with variously modified spines, but the delicate, intricate, lacework of the dorsal surface is a feature found only in the imaginal stage.
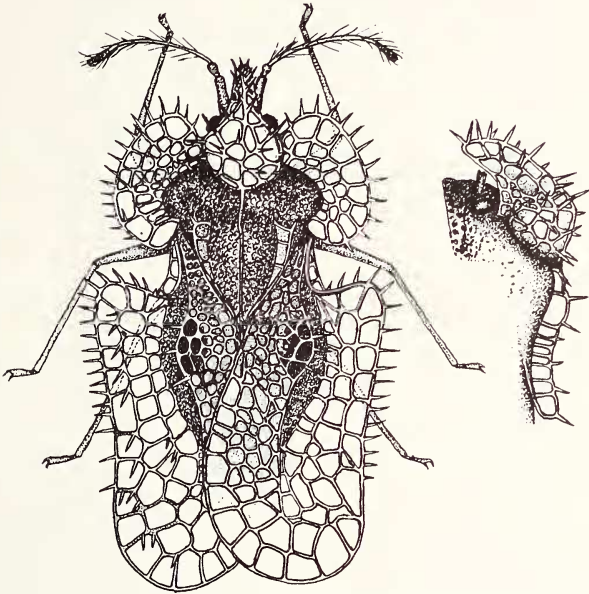
Fig. 71. *Corythucha erydictyonae* Osborn and Drake.

The most varied and most fantastic of the lacy formations arise from the collum, paranota, carinae, and posterior process of the pronotum. The hood of the collum unfolds in many different patterns, such as tectiform (figs. 34, 47, 53, 63), pyriform (fig. 71), subglobose to globose (figs. 43, 44, 68, 69), and huge elypsoidal inflations covering the entire pronotum (fig. 58). In many species the pronotal hood projects forward over the greater part or all of the head (figs. 53, 59, 68, 71). Formations of the paranota at times

Fig. 72. *Anommatocoris coleoptratus* (Kormilev).

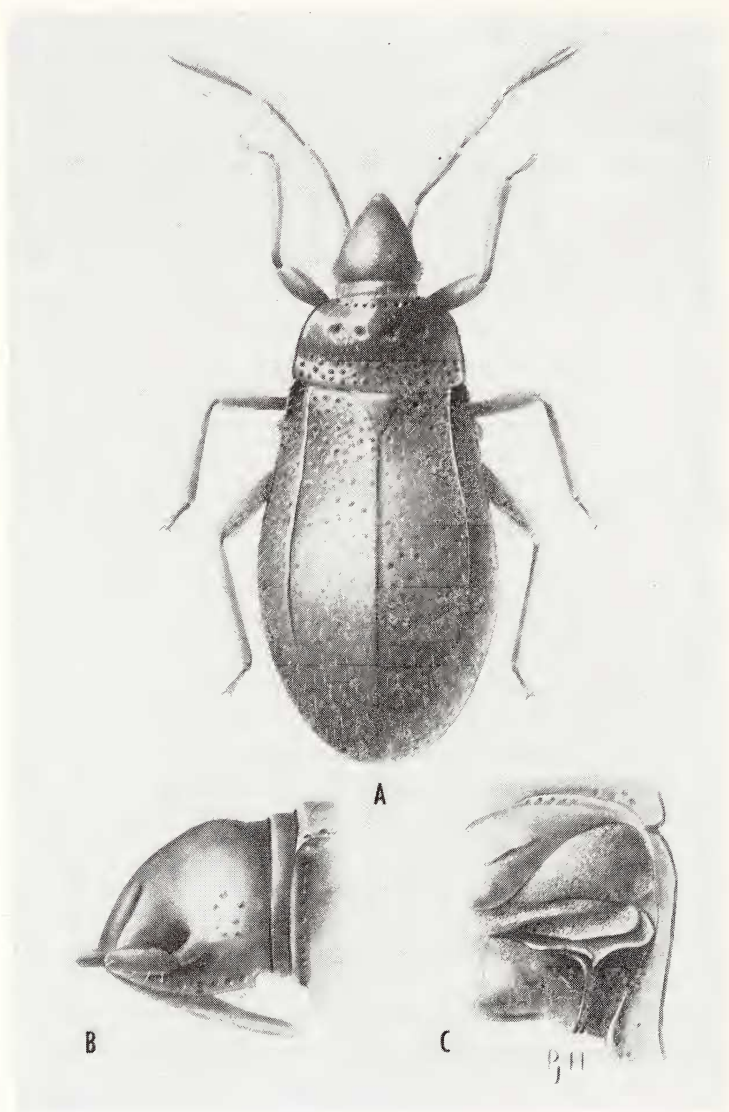are as bizarrely created and as gigantic in size as those of the collum. A few such oddities arising from the paranota are illustrated (figs. 34, 36, 37, 45, 55, 56). The carinae are not lacking in singularities as demonstrated in the figures (Figs. 43, 59, 62). In the genera *Aconchus* Horvath, *Dulinius* Distant, *Galeatus* Curtis, *Bako* Schouteden, *Aepycysta* Drake and Bondar (fig. 59), and *Hyalochiton* Horvath, the posterior process of the pronotum is areolate, tumid, and distinctly inflated. Towering formations of the hood (figs. 55, 57, 58) and paranota (figs. 55, 70) are found in a con-
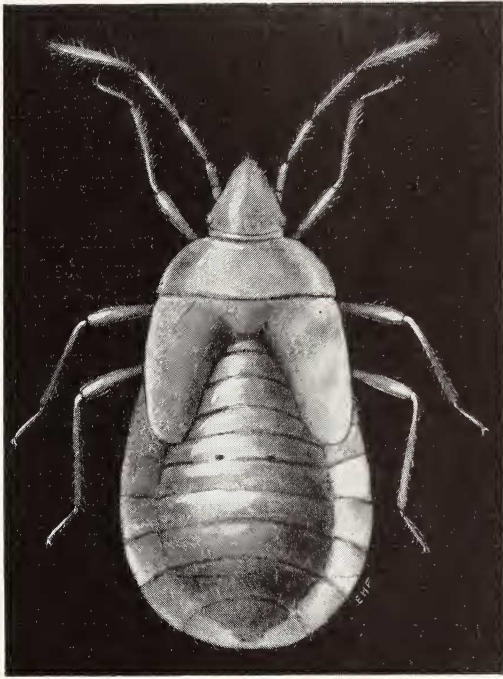

Fig. 73. *Anommatocoris coleoptratus* (Kormilev), nymph (last instar).

siderable number of genera. In some genera the elytra are slender (fig. 62), moderately wide (figs. 36, 41, 42) or extremely wide (figs. 38, 49, 61). The elytra are provided with a tumid inflation (largely the discoidal area) in a considerable number of species (figs. 34, 71).

83

Subfamily Vianaidinae Kormilev (**New Status**)

The Family Vianaididae was designated by Kormilev (1955) to hold a new genus and species, *Vianaida coleoptrata* (figs. 72, 73) from Argentina and another genus and species described by China (1945) as *Anommatocoris minutissima* (fig. 74), Family Lygaeidae, Subfamily Oxycareninae, from Trinidad, British West Indies. Kormilev placed the vianaidines in the Group Cimicomorpha and formed a table to show the structural similarities and dissimilarities between the vianaidines and tingids.

In the present study, we have found that the Genera *Anommatocoris* China (1945) and *Vianaida* Kormilev (1955) are inseparable from each other, and thus they are here synonymized, the former genus having priority by 10 years (**new synonymy**). Since the species *minutissima* and *coleoptrata* are clearly distinct from each other, the latter is here transferred to the Genus *Anommatocoris* (**new combination**). According to the *Régales*, Vianaidinae is the proper subfamilial name.

Since the species of vianaidines, in so far as known, are all myrmecophilous, they are naturally to be expected to have certain highly adaptive characteristics related to their very specialized, subterranean habitats.[4] These characteristics include their somewhat compressed, coleopteroid form, vestigial eyes, rather flattened pronotum; lack of spines, carinae, and other pronotal structures; elytral-like hemelytra which is punctate but without reticulations; and probably the unusual form of the metathoracic and dorsal abdominal glands. The Tingidae, as formerly constituted, generally do not have features of this sort, but since a parallel development of many of these characteristics often occur in unrelated Hemiptera living as inquilines in similar habitats, they cannot be considered to be valid familial criteria.

A further study of tingids and vianaidines as familial groups shows that certain differences thought to exist between them may

---

[4] Myrmecophilism is known to occur in the other subfamilies of the Tingidae. According to Hacker (1928), adults and nymphs of the cantacaderinae *Allocader leai* (Hacker) were collected in the nest of the host ant (*Amblyopone australis* Erich.) at Dunorban, Tasmania, and adults of the tingine *Lasiacantha leai* (Hacker) (descr. as *Myrmecotingis leai*, n. gen., n. sp.) from the nest of the dolichoderine ant (*Iridomyrmex conifer* Forel), Swan River, Western Australia. These two inquilines have fully-developed compound eyes.
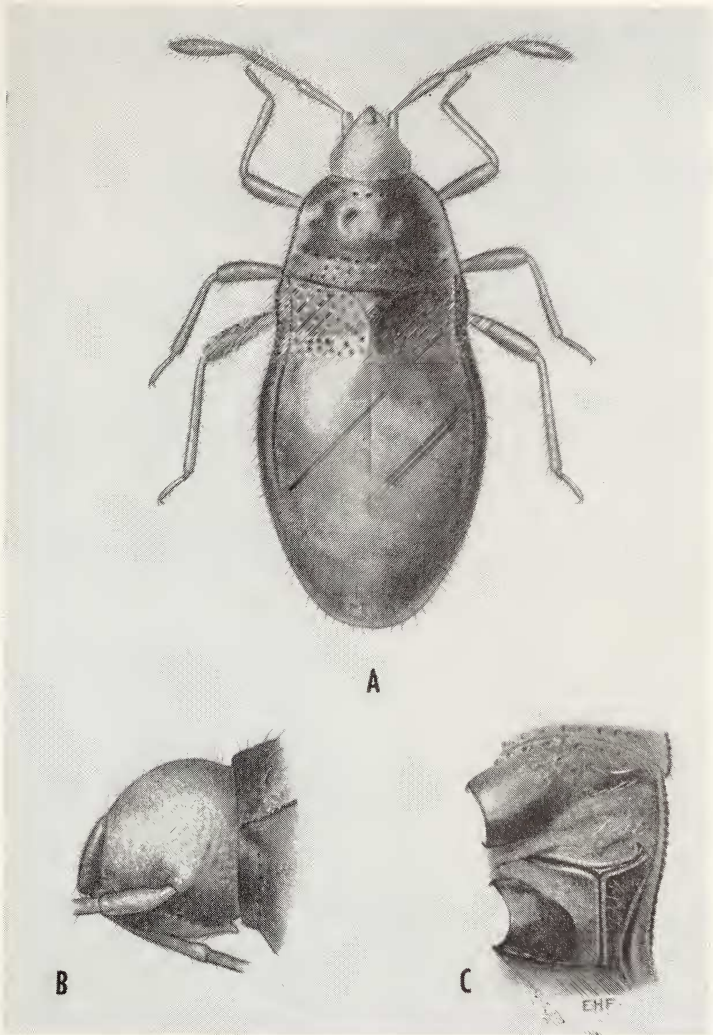
Fig. 74. *Anommatocoris minutissimus* China, **a**, dorsal and **b**, lateral aspects.

be discounted because there are so many exceptions. For example, unlike most tingids the labium of vianaidines extends beyond the hind coxae, but in cantacaderine tingids, such as species of the Genera *Teratocader* Drake, *Ceratocader* Drake (fig. 30), *Zetekella* Drake, *Allocader* Drake, *Phatnoma* Fieber, and *Cantacader* Amyot et Serville (fig. 28), the labium is long and extends onto or beyond the base of the metasternum. Among the extreme examples, the species *Allocader magnificus* Drake and *Nectocader gounellei* Drake have beaks that practically touch the first genital segment. In fact many of the cantacaderines have much longer beaks than those found in the vianaidines.

The Subfamily Tinginae presents a different labial picture. In this subfamilial group, the labium varies greatly in length, often among species in the same genus. In most tingines, however, the rostrum does not reach the metasternum, although there are many forms in various genera with beaks that extend more or less beyond the thorax onto the abdominal sterna. For example, in the tingine Genus *Ypsotingis* Drake (fig. 36), all of its seven known species have very long beaks that reach onto the sixth or seventh sternum of the abdomen. Thus, the length of the labium does not constitute a familial or even subfamilial character for the separation of vianaidids and tingids.

The vianaidines of all genera lack arolia. Although occasionally the tingids are said to have areola, these structures are also absent in both cantacaderines and tingines.

Certain purported differences between the vianaidines and tingids have arisen from misinterpretations of structures of each. The scutellum of vianaidines is distinct while in the Tingidae it is said to be generally lacking or vestigial but in fact in many genera it is merely concealed beneath the pronotum and in some Cantacaderinae it is exposed. Kormilev has indicated that the eighth sternum of female vianaidines, unlike that of the Tingidae, is a small subtriangular sclerite. However, this sclerite is actually a median extension of the seventh sternum (fig. 5, **SgP**) and equivalent to the subgenital plate of the Tingidae; the so-called eighth sternum (1st gonocoxopodites) is precisely the same in both groups.

Certain differences between vianaidines and tingids appear to be consistent. Kormilev points out that in the Tingidae the second antennal segment is always very short and the third segment is always the longest whereas in the vianaidids the segments increase in length from the first to the last. (Second and third antennal segments subequal in *A. minutissimus* China). He also pointed out

86

that the tingids have a scent gland ostiole with a vertical sulcus but that in the vianaidids the sulcus also has a horizontal branch (figs. 7, 72, 74). In the present study additional differences have been found. In the vianaidines the four abdominal sterna are fused while in the tingids only two or three are fused, and the vianaidines have a median endophallic diverticulum while it is paired in the tingids.

As opposed to these differences the tingids and vianaidines have many important features in common. The principal similarities (other than those applying to the Cimicomorpha generally) that Kormilev pointed out are that both have sternal carinae, two-segmented tarsi, unarmed femur and tibia, a distinctly four-segmented beak, bucculae, and both lack ocelli. Additional similarities have been uncovered in the present study. And one of singular interest is that the reservoirs of the metathoracic scent glands of vianaidines are relatively large, paired sacs as they are in tingids and are thus unlike the scent glands of any other of the Cimicomorpha. The vianaidines also share the following more or less distinctive features with the tingids. The ovipositor is a drilling type and lacks skeletal attachments to the first gonocoxopodites; the first gonocoxopodites are fused to the eighth paratergites; the ninth paratergites meet midventrally to cover the ovipositor and second gonocoxopodites; the parameres and phallus are symmetrical.

It is obviously desirable to give the vianaidines a taxonomic status consistent with that applied to comparable groups of other Heteroptera. As noted previously the vianaidines differ from the tingids in having certain highly adaptive characteristics related to their specialized habitat but such special characteristics are generally not regarded as valid for familial criteria. The vianaidines have certain other features such as the pattern of length of the antennal segments and distinctive scent gland ostiole, which serve to distinguish them from the tingids but these features are insufficient to warrant the status of a separate family for the vianaidines. In contrast the vianaidines share with the tingids a considerable number of distinctive characteristics as described above. Considered individually, these characteristics are probably not of very significant value, but as a group they constitute a character complex which strongly suggests relatively little divergence between the tingids and vianaidines. This veiw is further substantiated by the fact of their having in common, certain features not known in other cimicomorphs, such as the unique scent gland reservoirs and the special arrangement of the parts of the female genitalia and ninth parater-

87

gites. Consequently, the authors are compelled to conclude that the vianaidids should be classified as the Subfamily Vianaidinae in the Family Tingidae (**new status**).

Key to Genera and Species of Vianaidinae

1. Broadly obovate, widest slightly behind middle of elytra, the greatest width about two-thirds of median length; paranotum and costal area both wide and equally expanded, each with large, rounded punctures, the elytra also with large punctures; hypocostal lamina wide, obtusely angulately widened near base, with one complete row of large punctures and two rows deep in widest part of angle; compound eyes aberrant, triangular in outline, with 8 or 9 scattered facets, brachypterous form (fig. 75)

Thaumamannia manni, new genus & new species

Elongate-ovate, nearly three times as long as greatest width; paranotum and costal area very narrow, cariniform, each without punctures; hind pronotal lobe and elytra finely punctate; hypocostal lamina narrow, with one row of tiny punctures; compound eyes degenerate, with or without facets, brachypterous form .... 2.

2. Compound eyes with only a small cluster of facets; body scarcely constricted on lateral sides opposite scutellum; antennae with second segment slightly shorter than third segment (figs. 72, 73) .... *Anommatocoris coleoptratus* (Kormilev)

Compound eyes absent; body slightly constricted on lateral sides opposite apex of scutellum; antennae with second and third segments subequal in length, (fig. 74)

Anommatocoris minutissimus China

Genus Anommatocoris China

Anommatocoris China, 1945, p. 126.
Vianaida Kormilev, 1955, p. 468 (**new synonymy**).
Type species, *Anommatocoris minutissimus* China.

Elongate-ovate, shiny, smooth, with pubescent hairs. Head narrowed anteriorly, convex above, strongly deflected, without spines or processes; ocelli wanting; bucculae long, wide, as long as head beneath, slightly diverging posteriorly, punctate. Antennae inserted above middle of bucculae, moderately long, moderately stout, with some bristly hairs; segment one shortest, segment two slightly

shorter than or subequal to third; segment four longest, fusiform. Labium long, extending onto the third or fourth abdominal sternum. Pronotum depressed, impunctate on front lobe, punctate on hind lobe, slightly rounded behind; collar distinct, punctate; paranotum very narrow, carina-like. Scutellum triangular, impunctate. Metathoracic scent glands provided with ostiole and ostiolar sulcus on each metapleuron, with raised, prominent, ypsiliform sulcus, the evaporating area very large, with roughened surface, covering the entire metapleuron, hind part of mesopleuron, and thence ventrally onto their respective thoracic sterna to the labial sulcus.

Elytra entirely coriaceous, strongly convex, uniform in texture, with sides strongly deflexed downwards so as to conceal lateral sides and apex of abdomen; costal area very narrow, carina-like, non-punctate, clavus absent, fused with corium, not differentiated; corium not separated into areas, with a straight, longitudinal, carina-like vein running backwards slightly beyond middle of elytra, perhaps indicating boundary between subcostal and costal area, otherwise without boundary veins to indicate divisional areas. Male parameres symmetrical. Female ovipositor well developed. Abdomen buried deeply into the cavity formed by deflexed elytra. Legs moderately long, moderately stout, with some bristly hairs. Macropterous form unknown.

This genus comprised two species, both myrmecophilous and coleopteroid in appearance, with the elytra forming a straight commissure behind apex of scutellum. Morphological studies of the genus are included in the section on general morphology.

Anommatocoris coleoptratus (Kormilev) (Figs. 72, 73)
(**New Combination**).

Vianaida Kormilev, 1955, p. 468 (**new synonymy**).

This small, elongate-ovate, brownish species was described from a series of 25 brachypterous adults and 5 nymphs, all collected in the nest of a leaf-cutting ant, *Acromyrmex lundi* (Guérin), Rio Lujan, Tigre, Province of Buenos Aires, Argentina, by Mr. M. J. Viana. In addition to paratypes, we also have numerous nymphs and adults, collected by Mr. Viana at the type locality in the nests of the same species of ant. A paratype and a nymph, both taken in the same ant nest with the type, are figured. The convexity of the elytra is practically the same in *minutissimus* and *coleoptratus*. The adult is 1.80 mm. long.

Anommatocoris minutissimus China (Fig. 74)

Anommatocoris minutissimus China, 1945, 4 figs.

This elongate-ovate, reddish brown species was described from a series of specimens, taken in soil detrital silt, from the cacao experimental plantation of the Department of Botany, Imperial College of Tropical Agriculture, Trinidad, British West Indies. It is a myrmecophile, but the ant with which it is associated has not been determined. A paratype, kindly sent to us by Dr. W. E. China, is illustrated. The total length is 1.70 mm.

A. minutissimus is completely without compound eyes. Other species of vianaidines have degenerate compound eyes with only a few facets remaining, and these are possibly functionless. The other member of the genus, *A. coleoptratus* only has a small cluster of ommatidia. The characters used in the key and the illustrations distinguish these two congeners from each other. Both of these species can be easily separated from the new genus and species by their elongate-ovate form. The very narrow, carina-like paranota and costal areas are non-punctate. The hypocostal lamina is narrow and uniseriately punctate.

Genus *Thaumamannia*, new gen.

Brachypterous form: Broadly obovate, widest near middle of abdomen, strongly convex across elytra, subdepressed on front lobe of pronotum; hind pronotal lobe, paranota, elytra, and hypocostal laminae coarsely punctate. Coleopteriod in appearance, macropterous form unknown. Myrmecophile.

Head moderately long, sharply declivent in front, inserted into prothorax up to the compound eyes, without processes, spines, rugulae, and ocelli; tylus prominent, sharply demarcated; juga shorter and not as thick as tylus; bucculae long, wide, punctate, not extending forward beyond apex of tylus; labium extremely long, extending onto abdominal sterna; compound eyes atrophied, each with only eight or nine facets, which are not grouped together but separated from one another as individuals, and possibly functionless, the plate-like structure bearing the facets is triangular in outline with the acutely angulate apex slightly raised and projected forward a little beyond the antenniferous tubercles (fig. 75b); antennae moderately stout, with bristly hairs, with first segment not quite reaching to apex of head, second segment a little longer than first, other segments missing.

Pronotum without carinae, smooth, impunctate on fore lobe, coarsely punctate on hind lobe, with hind margin not extended
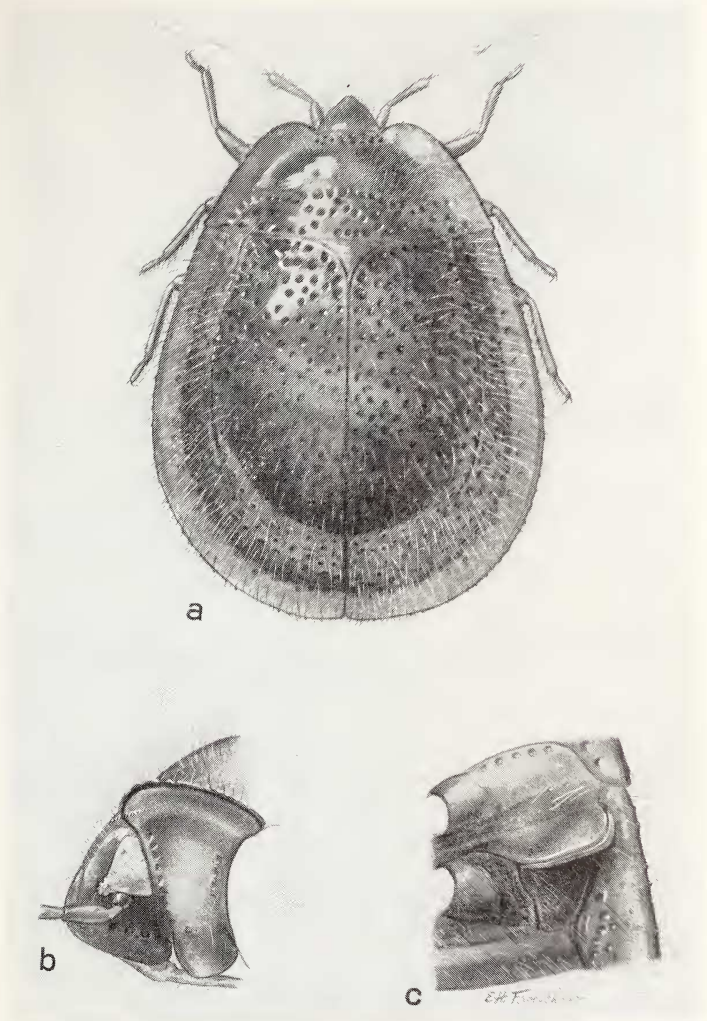
Fig. 75.   *Thaumamannia manni*, new gen. and new sp.

backwards and feebly roundly subtruncated; collum short, narrow, truncate in front, with two transverse rows of punctures; paranota widely explanate, mostly impunctate, with only a few punctures on inner posterior angles, finely serrate on exterior margin, subequal in width to that of the costal area. Scutellum moderately large, entirely exposed, triangular, impunctate, acutely angulate at apex. Metathoracic scent glands provided with prominent ostiole and large ostiolar sulcus, the sulcus distinctly arised, T-shaped, elevated, and the evaporating area very large, with roughened surface extending over all of metapleuron and posterior part of mesopleuron (fig. 75c) and thence ventrally on their respective sterna to labial channel.

Mesothoracic wings (fig. 75a) entirely coriaceous, strongly convex, deeply coarsely punctate, clothed with upright hairs, strongly deflexed downward so as to cover lateral sides and apex of abdomen, with commissure behind scutellum forming a straight line running down the middle of the back; costal area very wide, horizontally extended, with one row of large punctures, finely serrate on outer edge; corium not divided into areas, with a longitudinal, raised, straight, carina-like vein running backwards a little beyond middle of elytra, perhaps partly indicating boundary between subcostal and discoidal areas, discoidal, sutural, and claval areas not in the least indicated, no evidence of a membrane. Metathoracic wings obsolete. Abdomen deeply buried within the cavity formed by the strongly deflexed elytra, with ventral surface moderately clothed with short, reclining hairs. Female ovipositor well developed. Male unknown. Legs moderately long, moderately stout, unarmed, provided with bristly hairs; tarsi two-segmented, the first segment short.

Type species, *Thaumamannia manni*, n. sp. (fig. 75).

Easily separated from *Anommatocoris* China (= *Vianaida* Kormilev) by the broadly obovate form, very large punctures of pronotum and elytra, and the widely expanded paranota and costal areas.

Thaumamannia manni, new species (Fig. 75)

Small, obovate, reddish brown, with appendages brownish testaceous, labium testaceous; dorsal surface clothed with rather long, fine upright, whitish hairs, the abdomen beneath with much shorter, backward-inclined whitish hairs; hairs on appendages more bristly, fairly long, whitish. Width across widest part of abdomen nearly two-thirds of the median length. Length 2.00 mm., width (greatest) 1.45 mm.

Head above convex, strongly inclined downward anteriorly, without spines or tubercles; compound eyes degenerate, only 8 or 9 facets present, these separated from one another as individual facets with rounded instead of hexagonal lenses. Labium extending onto the third abdominal sternum. Dorsal surface smooth, slightly shiny, with fairly long, fine, erect, pale, hairy vestiture; punctures large, rounded.

Holotype, female, Santa Cruz, Bolivia, 1921–22, Dr. W. H. Mann, found in the nest of an ant. In U. S. National Museum. The type is illustrated (fig. 75).

This very interesting and singular genus and species are named in honor of Dr. William M. Mann, whose publications and collections have done so much to advance entomology from a worldwide aspect.

Literature Cited

Amyot, Charles J. & Serville, J. G. A. 1843. Histoire Naturelle des Insectes. Hémiptères. Paris. pp. lxvii + 675.

Baranowski, R. M. 1958. Notes on the biology of the royal palm bug, *Xylastodoris luteolus* Barber (Hemiptera, Thaumastocoridae). Ann. Ent. Soc. Amer. vol. **51**, no. 6, pp. 547–551.

Berthold, Arnold Adolph 1827. Latreille's naturliche Familien des Thierreichs. Weimar, Industrie-Comptoirs, x + 606 pp. (1st German translation from Latreille, Familles naturelles, 1825).

Billberg, Gustav Johann 1820. Enumeratio Insectorum in Museo Billberg. (Holmiae). Stockholm, Gadel. 138 pp.

Blöte, H. C. 1945. On the systematic position of *Scotomedes* (Heteroptera, Nabidae). Zool. Mededeelingen. vol. **25**, pp. 321–324.

Börner, Carl 1934. Uber System und Stammesgeschichte der Schnabelkerfe. Entom. Beih. Berlin. vol. **1**, pp. 138–144.

Brindley, M. D. 1930. On the metasternal scent glands of certain Heteroptera. Trans. Ent. Soc. London. vol. **78**, pp. 199–207.

Burmeister, Hermann 1835. Handbuch der Entomologie. Berlin, Th. Ch. F. Enslin. vol. **2**, iv + 400 pp.

Carayon, Jaques 1950a. Caractères anatomiques et postion systématique des Hémiptères Nabidae. Bull. Mus., Paris, 2 série, vol. **22**(1), pp. 95–101.

    1950b. Nombre et disposition des ovarioles dans les ovaires des Hémiptères—Héteroptères. Bull. Mus., Paris, 2 série, **22**(4), pp. 470–475.

    1954. Organes assumant les fonctions de la spermathèque chez divers Hètéroptères. Bull. Soc. Zool. France. vol. **79**, nos. 2–3, pp. 189–197.

    1955. Quelques caractères anatomiques des Hémiptères Aradidés. Rev. Française d'Entomologie, vol. **22**, fasc. 3, pp. 169–180, 3 pls.

    1958. Études sur les Hémiptères Cimicoidea—I. Mem. Mus. National Hist. Nat., serie A, vol. **16**, fasc. 5, pp. 141–172, 18 figs.

Carayon, Jacques, Usinger, Robert and **Wygodkinsky, P.** 1958. Notes on the higher classification of the Reduviidae, with the description of a new tribe of the Phymatinae (Hemiptera-Heteroptera). Rev. Zool. Bot. Afr., vol. **57**, fasc. 3–4, pp. 256–281, 66 figs.

Champion, George C. 1897. Rhynchota, vol. **2**, pp. 1–32 *in* Godman and Salvin, Biologia Centrali-Americana. London.

China, William E. 1933. A new family of Hemiptera-Heteroptera with notes on the phylogeny of the suborder. Ann. Mag. Nat. Hist. ser. 10, vol. **12**, pp. 180–196.

1943. The generic names of the British Hemiptera-Heteroptera, with a check list of the British species. *In* The generic names of British Insects, pt. 8, pp. 211–342. Roy. Ent. Soc. London.

1945. A completely blind bug of the family Lygaeidae Hemiptera Heteroptera). Proc. Roy. Ent. Soc. London, vol. **14,** nos. 9–10, pp. 126–128, 1 fig.

1953. A new subfamily of Microphysidae (Hemiptera-Heteroptera). Ann. Mag. Nat. Hist. ser 12, vol. **6,** p. 67–74, 3 figs.

1955. A reconsideration of the systematic position of the family Joppeicidae Reuter (Hemiptera-Heteroptera), with notes on the phylogeny of the suborder. Ann. Mag. Nat. Hist. ser. 12, vol. **8,** pp. 353–370, 4 figs.

China, William E. and Miller, N. C. E. 1955. Check-list of family and subfamily names in Hemiptera-Heteroptera. Ann. Mag. Nat. Hist., ser. 12, vol. **8,** pp. 257–267.

1959. Check-list and keys to the families and subfamilies of the Hemiptera-Heteroptera. Bull. British Mus. (Nat. Hist.) Entomology, vol. **8,** no. 1, pp. 1–45, 1 fig.

China, William and Myers, J. G. 1929. A reconsideration of the classification of the Cimicoid families (Heteroptera) with the description of two new spider web bugs. Ann. Mag. Nat. Hist. ser. 10, vol. **3,** pp. 97–125.

Costa, Achille 1838. Cimicum Regni Neapolitani Centuriae. Napoli. Cent. 1, 76 pp.

1855. Cimicum Regni Neapolitani. Centuria Tertia et quartae. Attei del Reale Instituto d'Incoraggiamento alle Scienze Naturali di Napoli. vol. **8,** pp. 225–300.

1860. Additamenta ad Centurias Cimicum Regni Neapolitani. Napoli. 41 pp. 3 pls.

Davis, Norman T. 1955. Morphology of the female organs of reproduction in the Miridae (Hemiptera). Ann. Ent. Soc. Amer. vol. **48,** no. 3, pp. 132–150, 20 figs.

1956. The morphology and functional anatomy of the male and female reproductive systems of *Cimex lectularius* L. (Heteroptera, Cimicidae). Ann. Ent. Soc. Amer. vol. **49,** no. 5, pp. 466–493, 30 figs.

1957. Contributions to the morphology and phylogeny of the Reduvioidae (Hemiptera: Heteroptera). Part 1. The morphology of the abdomen and genitalia of Phymatidae. Ann. Ent. Soc. Amer. vol. **50,** no. 5, pp. 432–443, 21 figs.

Distant, William L. 1909. New Oriental Tingididae. Ann. Soc. Ent. Belgique, vol. **53,** pp. 113–123.

Douglas, John W. and Scott, John 1865. The British Hemiptera. London, J. E. Adlard. vol. 1, 627 pp., 21 pls.

Drake, Carl J. and Davis, Norman T. 1958. The morphology and systematics of the Piesmatidae (Hemiptera), with keys to world genera and American species. Ann. Ent. Soc. Amer. vol. 51, no. 6, pp. 567–581, 34 figs.

Drake, Carl J. and Poor, Margaret 1936. The genera and genotypes of Tingitoidea of the Western Hemisphere. Iowa State Coll. Jour. Sci., vol. 10, no. 4, pp. 381–390.

Drake, Carl J. and Ruhoff, Florence A. in press. Chorology, type species and synonymy of the genera of Tingidae (Hemiptera) of the world.

Drake, Carl J. and Slater, James A. 1957. The phylogeny and systematics of the family Thaumastocoridae (Hemiptera: Heteroptera). Ann. Ent. Soc. Amer. vol. 50, no. 4, pp. 353–370, 2 figs.

Duméril, André Marie Constant 1806. Traite elementaire d'histoire naturelle. Paris. an. XII (1804). German transl.: ''Anfangsgründe der Naturgeschichte zum Unterricht in den Lyceen, aus dem Franz. mit Zusätzen u. Verbesserungen.''

Fabricius, Johann C. 1803. Systema Rhyngotorum secundum ordines, genera, species adjectis synomymis, locis, observationibus, descriptionibus. Brunsvigae. 314 pp.

Fallén, Carl F. 1814. Specimen novam Hemiptera disponendi methodum exhibens. Lund, Berling. 26 pp.

1829. Hemiptera Sueciae. Cimicides eorumque familiae affines. (pp. 1–16 published June 6, 1828, the remainder in 1829). Lund, Berling. 186 pp.

Ferrari, Pietro M. 1874. Hemiptera agri Ligustici. Ann. Mus. Civ. Stor. Nat. Gen. ser. 1, vol. 6, pp. 116–208.

Fieber, Franz X. 1844. Entomologische Monographien. 136 pp. 10 pls.

1851. Genera Hydrocoridum secundum ordinem naturalem in familias disposita. Abh. bohm. Ges. Wiss. Prag. vol. 7, pp. 181–212.

1861. Die Europaischen Hemiptera. Halbflugler (Rhynchota Heteroptera). Wien, Gerold. 444 pp. 2 pls.

Flor, Gustav 1860. Die Rhynchoten Livlands in systematischer Folge beschrieben. Arch. Naturk. Liv–, Ehst–, und Kurlands. vol. 3, pp. 1–825.

Galliard, H. 1935. Recherches morphologiques et biologiques sur la reproduction des Réduvidés hematophages (*Rhodnius* et *Triatoma*). These Fac. Sc. Paris, ser. A, n. 1554, 160 pp.

Hacker, H. 1928. New species and records of Australian Tingitoidea (Hemiptera). Mem. Qd. Mus. vol. 9, pp. 174–188.

Horváth, Geza 1906. Synopsis Tingitidarum Regionis Palaearcticae. Ann. Mus. Hist. Hungarici, vol. 4, 118 pp., 1 pl. (color).

1911. Nomeclature des families des Hemipteres. Ann. Mus. Nat. Hungarici, vol. 9, 34 pp.

Hurd, Margaret Poor 1946. Generic classification of North American Tingoidea (Hemiptera-Heteroptera). Iowa State Coll. Jour. Sci., vol. 20, no. 4, pp. 429–493.

International Commission on Zoological Nomenclature

1943. Opinions rendered by the International Commission on Zoological Nomenclature, vol. 2, pp. 81–99. (Opinion 143).

1954. Opinions and declarations rendered by the International Commission on Zoological Nomenclature. vol. 2, no. 53, Direction 4, pp. 629–652.

Kirkaldy, George W. 1906. Notes on the classification and nomenclature of the Hemipterous superfamily Miroidea. Canadian Ent. vol. 38, pp. 369–376.

1908. Some remarks on the phylogeny of the Hemiptera-Heteroptera. Canadian Ent. vol. 40, pp. 357–364.

Kolenati, Friderico A. 1856. Meletemata entomologica Hemipterorum Heteropterorum Caucasi. Harpagocorisiae, monographice dispositae. Bull. Soc. Nat. Moscou, vol. 29, pp. 419–502, 3 pls.

Kormilev, Nicolas A. 1955. A new Myrmecophil family of Hemiptera from the delta of Rio Paraná, Argentina. Rev. Ecuat. Ent. Paras., vol. 2, nos. 3–4, pp. 465–477, 1 pl.

Kullenberg, B. 1947. Über Morphologie und Funktion des Kopulationsapparats der Capsiden und Nabiden. Zool. Bidr. Uppsala, vol. 24, pp. 217–418, 85 figs. 23 pls.

Laporte, Francis de Comte de Castelnau 1833. Essai d'une classification systématique de l'ordre des Hémiptères (Hémiptères Hétéroptères, Latr.). *In* Guerin Magasin de Zoologie. vol. 2, pp. 1–88, 4 pls.

Latreille, Pierre A. 1807. Genera Crustaceorum et Insectorum secundum ordinem naturalem in familias desposita. Paris, Konig. vol. 2, 289 pp.

1810. Considérations générales sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides, et des Insectes. Paris, Schoell. 444 pp.

1825. Familles naturelles du regne animal. Paris, Bailliere. 570 pp.

1829. Les Crustaces, les Archnides et les Insects distribues en familles naturelles. pts. 1–2 *in* Cuvier, G. C., Le Régne Animal. 2d ed. Paris, Deterville. vol. **4–5**, 556 pp.

Leston, Dennis, Pendergrast, John G. and Southwood, T. R. E. 1954. Classification of the terrestrial Heteroptera (Geocorisae). Nature. vol. **174**, pp. 91–92.

Lethierry, Lucien and Severin, Guillaume 1896. Catalogue general des Hémiptères. Berlin. vol. **3**, pp. 1–275.

Linnaeus, Carl 1746. Fauna Suecica. Stockholm, Laur. Salvii. 411 pp.

1758. Systema Naturae. ed. 10, Stockholm, Laur. Salvii. 823 pp.

McAtee, W. L. and Malloch, J. R. 1924. Some annectant bugs of the superfamily Cimicoideae (Heteroptera). Bull. Brooklyn Ent. Soc., vol. **19**, no. 3, pp. 69–82, 1 pl.

1925. Another annectant genus (Hemiptera; Cimicoidea). Proc. Biol. Soc. Washington. vol. **38**, pp. 145–148, 6 figs.

Monte, Oscar 1947. Gêneros e genótipos dos Tingídeos do Mundo. Papeis Avulsos Dept. Zool. Sao Paulo., vol. **8**, No. 1, pp. 1–22.

Oshanin, B. 1908. Verzeichnis der palaearctischen Hemipteren mit besonderer Berucksichtigung ihrer Verteilung im russichen Reiche. Ann. Mus. Zool. St. Petersbourg. vol. **1**, pt. 2, pp. 395–586.

1912. Katalog der palaarktischen Hemipteren (Heteroptera, Homoptera-Auchenorhyncha and Psylloideae). Berlin. 187 pp.

Pendergrast, J. G. 1957. Studies on the reproductive organs of the Heteroptera with a consideration of their bearing on classification. Trans. Roy. Ent. Soc. London, vol. **109**, pt. 1, pp. 1–63, 122 figs.

Poisson, Raymond 1951. Ordre des Hétéroptères. *in* Grassé, Traité de Zoologie. vol. **10**, pp. 1657–1803.

Puton, Auguste 1879. Synopsis des Hémiptères Hétéroptères de France. Paris. vol. **1**, pt. 2, pp. 83–159.

1899. Catalogue des Hémiptères (Héteroptères, Cicadines et Psyllides) de la faune palearctique. Caen. 4th ed. 121 pp.

Reuter, Odo M. 1910. Neue Beiträge zur Phylogenie und System-atik der Miriden nebst einleitenden Bemerkungen über die Phylogenie der Heteropteren-Familien. Acta Soc. Sci. Fennicae. vol. **37**, no. 3, pp. 1–167.

1912. Bemerkungen über mein neues Heteropteren-system. Öfv. Finska Vet. Soc. Förh. vol. **54A**, no. 6, pp. 1–62.

Sahlberg, Reginald 1848. Monographia Geocorisarum Fenniae. Helsingfors. 155 pp.

Schiödte, J. C. 1870. Nogle nye Hovedsaetninger af Rhynchot-ernes Morphologi og Systematik. Naturh. Tidsskr. vol. **6**, pp. 237–266 (1869); (translated into English Ann. Mag. Nat. Hist. vol. **6**, pp. 225–249. (1870).

Siebke, Johann Heinrich 1874. Enumeratio Insectorum Nor-vegicorum, Fasciculus 1, Catalogum Hemipterorum et Orthopterorum continens, vii + 334 pp.

Singhi-Pruthi, H. 1925. The morphology of the male genitalia in Rhynchota. Trans. Ent. Soc. London **1925**, pp. 127–257.

Spinola, Maximilien. 1837. Essais sur less genres d'Insectes ap-partenants à l'ordre des Hémiptères L. ou Rhyngotes F. et à la section des Hétéroptères Duf. Gênes, Yves Graviers. 383 pp.

1840. Essai sur les insectes Hémiptères, Rhyngotes, ou Hétéroptères. Paris. 383 pp.

1850. Tavola sinottica dei generi spettanti alla classe degli insetti arthrodignati Hemiptera. Mem. Matem. Fis. Soc. Italiana Modena. vol. **25**, pp. 43–100.

Stål, Carl 1859. Hemiptera. Species novas descripsit. Kong-lika Svenska Fregattens Eugenies resa omkring jorden. vol. **3** (Zoologi, Insekter), pp. 219–298.

1865. Hemiptera Africana. Stockholm. vol. **3**, pp. 1–200.

1870. Hemiptera insularum Philippinarum. Bidrag till Philipppinska öarnes Hemiptera-fauna. Öfv. Svenska Vet.-Ak. Förh. vol. **27**, no. 7, pp. 607–776.

1873. Enumeratio Hemipterorum. Svenska Vet.-Ak. Handl. vol. **11**, no. 2, pp. 1–163.

1874. Genera Tingitidarum Europae disposuit. Öfv. Svenska Vet.-Ak. Föhr. vol. **31**, no. 3, pp. 43–59.

Takeya, Choku 1951. A tentative list of Tingidae of Japan and her adjacent territories (Hemiptera). Kurume Univ. Jour. (Nat. Sci.). vol. **4**, no. 1, pp. 5–28.

Tanaka, Takayoshi 1926. Homologies of the wing veins of the Hemiptera. Annotationes Zoologicae Japonenses, vol. **11**, pp. 35–57, 2 pls.

Tullgren, Albert 1918. Zur Morphologie and Systematik der Hemipteren I. Entomologisk Tidskrift, vol. **39**, no. 2, pp. 113–132, 11 figs.

Uhler, Philip R. 1886. Check list of the Hemiptera Heteroptera of North America. Brooklyn, H. H. Kahrs. 32 pp.

Van Duzee, Edward P. 1916. Check list of the Hemiptera of Mexico. New York, New Era Printing Co. 111 pp.

1917. Catalogue of the Hemiptera of America north of Mexico excepting the Aphidae, Coccidae, and Aleurodidae. Univ. Calif. Pubs. Ent. vol. **2**, 902 pp.

Vollenhoven, S. C. Snellen van 1878. Hemiptera Heteroptera Neerlandica de inlandsche ware Hemipteren beschreven en meerendeels ook afgebeeld. s'Gravenhage, Martinus Nijhoff. 368 pp., 22 pls.

Westwood, John O. 1840. An introduction to the modern classification of insects. London, Longman *et al*. 587 pp.